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A Monograph of the Nearctic Plagiochilaceae

Part III. Sectio Contiguae to Conclusion.*

RUDOLF M. SCHUSTER

Duke University, Durham[1]

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Sectio VIII. Contiguae Carl

Plants sparsely branched, the branches (in our species) on weak shoots usually monopodial, intercalary, diffuse, but on *mature shoots often* 2-4 × *pseudodichotomously furcate* and terminal in origin. *Plants green* becoming slightly brownish with age in some species, *usually dull,* medium sized (2-3.3 mm wide) to robust (3.5-5 mm wide). Stem with cortex 2-3 (-4) stratose, firm, of thick-walled, elongate cells. Leaves varying from contiguous to weakly imbricate, laterally patent when moist, firm and usually relatively opaque, broadly to narrowly *ovate or ovate-falcate,* the antical margin nearly straight to concave normally; the *postical margin strongly to moderately ampliate* (at least just above base), the widest point just above the leaf-base; leaf-width varying from *ca.* 1.2 to 2.2 *the leaf-length;* line of insertion of the leaves elongate, the leaves rather *long-decurrent dorsally,* but relatively *short-decurrent* (*ca.* 0.2 × the merophyte length) *postically,* the decurrent strip *not or narrowly and obscurely reflexed, edentate,* not forming a water sac or prominent crista; leaves distinctly dentate to spinose-dentate (rarely nearly edentate in *P. aspleniformis* and *dubia*), usu-

* Two previous sections of this work have appeared in *The American Midland Naturalist,* **62**(1):1-166; **62**(2):257-395. This is the terminal section and contains the references for the entire monograph.

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ally with 1-2 teeth near apex of antical margin (the edentate portion of antical margin more or less reflexed; the cnemis moderately distinct to well-defined), with 2-several teeth at the often subtruncate apex, and with 2-6 teeth on the postical margin. *Cells medium sized, ca.* 18-24 μ wide medially, with small or minute to distinctly bulging trigones; oil-bodies formed of protuberant, coarse globules, appearing coarsely papillose or segmented, mostly 3-6 per cell, but rarely to 11 per cell, moderately large (to 5 x 10 μ). *Underleaves vestigial,* of 1-several short cilia. Asexual reproduction *usually present, by leafy propagula* formed on the postical face (more rarely, and to a lesser degree, also on the antical face) of the leaf.

Female plants (where known) with a short, included perianth, obdeltoid to obcuneate in lateral view, the ciliate mouth nearly or quite as wide as the dorsal keel is long; *dorsal and ventral keels subequal in length* (at least when perianth is juvenile); dorsal keel usually (always?) winged, at least at base.

The present section is closely allied to the Sectio Yokogurenses and the Sectio Hypnoides. The first of these, including only *P. yokogurensis,* differs from the present group of species in the more copiously pseudodichotomous branching, and in the caducous distal halves of the leaves. The second of these groups, Sectio Hypnoides, is separated from the present complex by the cristate postical leaf-bases, which are normally strongly reflexed and often more or less dentate, by the denser leaves, and by the development of lamellate underleaves.

These three sections are similar in the essentially ovate or ovate-falcate leaves, in the ability of their species to produce leafy propagula, as well as in the basically similar oil-bodies of all species concerned, in the laterally spreading (never postically secund) leaves, in the limited number of teeth (usually less than 15-20) the leaves are able to produce, in the basically similar cell-size of most of the species, in the lack of a basal vitta, and in the apparent inability of their species to produce sporophytes. Of these three sections, the present one appears to be by far the least specialized (and possibly stands ancestral to the two others). The Sectio Yokogurenses appears to be derived by the development of more fragile leaves, which develop the ability to fragment; the Sectio Hypnoides and Sectio Crispatae appear to have been derived by the greater elaboration of the postical base and the greater decurrence of the postical margins. Some members of the Hypnoides and Crispatae are transitional and thus make a separation difficult to maintain. However, all the Contiguae have minute, often ephemeral underleaves, while the Hypnoides and Crispatae mostly possess large and distinct underleaves. These two sections, furthermore, have much more closely imbricate leaves than the Contiguae.

Branching in the Contiguae is quite diverse and needs to be intensively studied. It is clear that in some species (*P. dubia, P. virginica, P. floridana* and *P. aspleniformis*) there are frequent or at least occasional "pseudodichotomous" branches, *i.e.,* terminal branches where the main axis is laterally displaced so

that the main shoot appears once or repeatedly furcate (see Fig. 55A:1, *P. floridana;* Fig. 56:3, *P. aspleniformis*), although branches may arise largely in an axillary position, from older shoot sectors, as intercalary branches. In the presence of terminal branches the Contiguae approach the Yokogurenses, where pseudodichotomous, furcate branching is common, although axillary branches are also common in the one species of that section studied. The Contiguae also approach, in this respect, the Parallelae, which are characterized by a regular furcate, decompound branching (see Schuster 1959a, Fig. 41:6, *P. diffusa*). These three sections are further characterized by having perianths with the mouth truncate at nearly right angles to the axis, or with the mouth only slightly oblique — thus with the postical keel nearly or quite as long as the antical; and by the ability to develop propagula. The first of these last two characteristics is shared with several preceding sections (Choachinae, Bidentes, Asplenioides, Zonatae), which, however, never or only abnormally produce terminal branches. The ability to produce propagula is shared with the Hypnoides and Crispatae, sections in which the perianth-mouth is typically strongly obliquely terminated with an abbreviated postical keel.

PLAGIOCHILA VIRGINICA Evans
Figs. 43-48

Plagiochila virginica Evans, *in* Millspaugh, Flora of West Virginia 497, 1892; Evans, Bot. Gaz. 21:190, 1896, in part (West Virginia plants only).

Plants growing in intertwined patches, the rhizomatous stems often ± leafy, creeping, giving rise to distant to closely approximated, simple or on mature shoots commonly dichotomous aerial stems, *plants green to deep green, dull, without brownish pigmentation.* Leafy shoots when mature (2.5) 2.75-3.2 mm wide, occasionally 3.5-3.8 (4.0-4.8) mm wide and *ca.* 1.3-2.0 cm long, occasionally to 3 cm long. Stems from a minimum of *ca.* 150-165 to 190-250 μ, occasionally 400-430 μ wide; with cortex (type) green to brownish, scarcely thick-walled (bistratose); on robust plants (stem to 430μ wide) cortex strongly brownish, 2-3 stratose, the cortical cells ± tangentially flattened, thick-walled, brownish, (13) 14-16.5 μ wide; medulla varying from 6-7 to 12-14 cells high depending on robustness of stem, of ± thin-walled, pellucid cells, (18) 21-27 (30) μ in diameter. Branches on weak plants exclusively monopodial and intercalary, few or none from leafy aerial shoots; on robust ♀ plants aerial shoots commonly once or twice furcate, the branches terminal in origin. Rhizoids infrequent, except at bases of aerial stems, but occasionally on some aerial stems, which may become decumbent and rhizoidous. Leaves *approximate to moderately imbricate, widely spreading* (*ca.* 60-80°), essentially obliquely, asymmetrically, *rather broadly ovate,* their line of insertion slightly arched acroscopically, but the *postical base exceedingly short-decurrent* (*the stem consequently usually very considerably exposed, in postical aspect*); antical base moderately decurrent; leaves *ca.* 1050-1100 (1250-1400) μ wide x 1500-1650 (1700) μ long, occasionally to 1500-1600 μ wide x 1900-2050 μ long (1.25-1.45 [1.6] × *as long as wide*), widest *shortly above the base;* postical margin arched, (*but often only moderately dilated basally*), the antical margin nearly

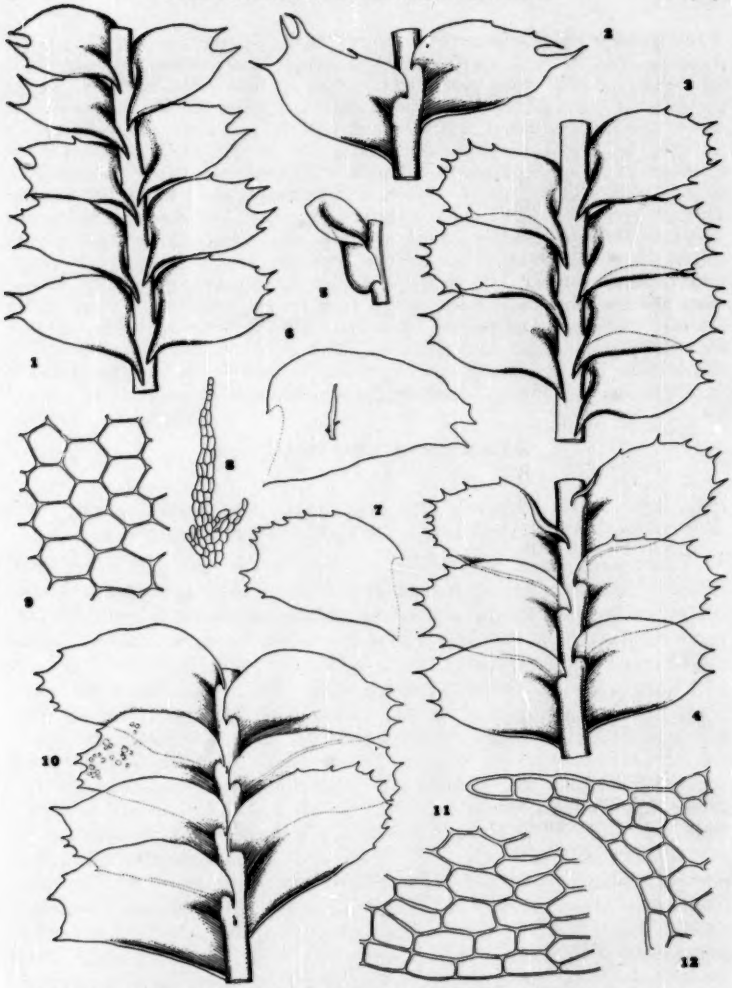

Fig. 43.—*Plagiochila virginica* Evs.. 1. Weak shoot, antical aspect (x *ca.* 20); 2. Sector of atypical, weak shoot, postical aspect (x 16); 3-4. Sectors of most robust extreme seen of type plants, antical and postical aspects (3, x 19; 4, x 15); 5. Atypical male bract from rudimentary androecium (x *ca.* 8); 6. Large leaf, and to same scale, associated underleaf (x 16); 7. Medium-sized leaf (x 16); 8. Underleaf (x 58); 9. Median cells (x 175); 10. Postical aspect of shoot-sector, the propagula-initials drawn in on one leaf only (x 16); 11. Cells of postical leaf base (x 180); 12. Tooth near leaf-apex (x 175). (Figs. 1-4 from type of *P. virginica;* 5-12, from plants collected at Island Home, e. of Knoxville, Tenn., *Sharp* 34339.)

straight or with basal 1/4 to 1/3 (rarely 1/2) reflexed (thus often appearing concave in profile), the distal portion straight to slightly convex; *postical base not or scarcely, narrowly erect, not usually reflexed;* antical margin entire, except near apex (where occasionally with 1-2 teeth); postical margin usually subentire or entire, except on distal ½ to ¼ (where with 1-5 small, scarcely spinose teeth); apex with 2-5 (6) obtuse to spinose teeth, occasionally with two larger and evidently lobe-like; *teeth small and short,* usually 2-3 cells high and 1-2 cells wide at base to 4-5 cells long and 3-5 cells wide at base, the apex often of two single, nearly isodiametric cells in a row; the *margin as a whole with usually* 4-10 *teeth,* but on juvenile leaves often only the two apical, lobe-like teeth discrete. Cells slightly (type) to distinctly collenchymatous, the apical from *ca.* 18-20 μ (type) to 20-24 (rarely 24-28) μ; the marginal cells along apical half of postical margin *ca.* 16-19 (21) μ; the *median cells ca.* (21) 23-25 (26) x 23-32 (35) μ; basal cells not or scarcely evenly thick-walled; cells at postical base 1.3-2.5 × as long as wide, *ca.* (12) 14-17 x 21-26 (30-38) μ up to 18-20 x 32-40 μ, with longitudinal walls not very prominently thick-walled; oil-bodies 8-12 per cell in most median cells, mostly 2 x 4.5 μ to 2.5 x 5 μ, but occasionally to 3 x 7 μ or even 2-3 x 8-9 μ, *formed of coarse segments* (usually a row of 2-5 globules forming an oil-body, sometimes with the median part of the oil-body of 2 rows of segments), each *ca.* 1.8-2.2 μ in diameter; in a few cells oil-bodies largely homogeneous, or 2-3 segmented, and only 2.5-4 μ in diameter (then smaller than chloroplasts); chloroplasts normally *ca.* 4-5.5 μ in longer diameter. *Underleaves appearing absent* (reduced to stalked or unstalked slime-papillae) *or minute* (of 1-2, occasionally 3-5, ciliary segments terminated by slime papillae), occasionally lanceolate. *Asexual reproduction by means of propagula from the postical leaf-surface.*

Dioecious. Usually sterile. Male plants very rare; the bracts (perhaps not fully developed) with concave, erect base, somewhat flaring apex, the margins entire or ending in a blunt tooth. Female plants rarely developed, usually more robust (to 4.5-5 mm wide x 2.5-3.5 cm long) and occasionally pseudodichotomously furcate. Bracts ovate-rectangulate, the strongly reflexed antical margin nearly straight, the *apex commonly broadly subtruncate,* the postical margin rather strongly dilated above base but nearly straight distally, varying from 1400 μ long x 1000-1150 μ wide to 1500 μ long x 1200-1225 μ wide (averaging slightly smaller than robust leaves), undulate on the postical margin, *strongly and irregularly serrate-dentate to spinose-dentate,* the postical margin with 5-7 or 10-14 coarse and irregular teeth, the truncate apex with 2-4 irregular, coarse teeth, the *antical margin edentate* or with a single preapical tooth. Perianth (juvenile only known) obdeltoid in lateral profile, compressed laterally, *antical keel not or hardly longer than postical,* the antical keel *in basal half with a weak lamellate carina* that is edentate, the rounded-truncate mouth coarsely but not closely dentate, the *teeth not spinose* (terminal cells mostly 13-15

x 20-23 μ, not strongly attenuate; subterminal cells nearly or quite isodiametric), the teeth broad-based, commonly 3-6 cells wide at base x (4) 5-10 cells long, *the apex uniseriate for a length of only* 1-2 *cells.*

Type.—Beaver Spring, near Mercer, West Virginia (*F. Millspaugh* 1550), 1890; type in Yale Herbarium!; cotype in Herbarium of NYBG!

The preceding description is based in part on sterile plants of the type (a mod. *parvifolia-viridis-leptoderma*), from which the minimal measurements are derived, in part from more robust plants, more typical of the species, of *Schuster* 37625. From this the gynoecial data are derived, as well as the maximal measurements given.

Distribution.—Imperfectly known, but apparently ranging in the upper edge of the Piedmont and lower elevations of the Appalachian Plateau from Virginia and West Virginia to northern Georgia, and northeastern Mississippi at elevations of usually 1800-3000 ft.; southward to the juncture of the Interior Plateau region and the inner Coastal Plain, in N.E. Mississippi (there at an elevation below 750 ft.!).

WEST VIRGINIA: In Limestone cave, Beaver Springs, near Mercer, May 25, 1892 (*C. F. Millspaugh* 1550! *type*), *Isotype* examined in NYBG! VIRGINIA: Sinking Creek at base of Salt Pond Mountain; on vertical shaded limestone, rocky outcrop near water, at spring outlet to Harvey's Cave (*Patterson* 1426!); deep gorge of Big Devil's Stairs, Shenandoah Ntl. Park, Rappahannock Co., on noncalcareous rocks (*Patterson* 2205!); The Cascades near Hot Springs, Bath Co., on limestone (*Patterson* 1448!); NE. side of Bent Mt., on rock in woods, 2500 ft., Roanoke Co. (*Patterson and Sharp R*-311!); base of gorge at the Pinnacles, Dan R. Gorge, Patrick Co. (*Patterson and Anderson* 1375 p. p., with *Frullania squarrosa*); Cascades, 2900 ft. and lower, Little Stony Cr. near Mt. Lake, Giles Co. (*Schuster* 40202, 40236); Limestone cliff 3 mi. SE. of Bluegrass, Highlands Co. (*Patterson* 2441!; transitional to var. *caroliniana*); Marty Branch, Dismal R., Buchanan Co., on Gladeville Sandstone (*Patterson* 2584!; somewhat atypical, the subapical cells often only 12-16 μ; postical cells elongated, their longitudinal walls $\pm$ thick-walled; a somewhat leptodermous var. *caroliniana*?). Also reported from Giles and Buchanan Cos. (Patterson, 1955). The previous report of this species from Virginia (in Patterson, 1950) is incorrect and is referable to *P. yokogurensis* subsp. *fragilifolia.* NORTH CAROLINA: Linville Caverns, near outlet of spring, moist limestone (associated, nearby, with *Plagiochasma wrightii* and the ferns *Camptosorus rhizophyllus* and *Asplenium cryptolepis*), on Rte. 221, McDowell Co. (*Schuster* 29058, 28814); same locality, but on exposed, dry, calcareous cliff, associated with *Frullania squarrosa* and *Radula complanata,* and the xerophytic ferns, *Asplenium cryptolepis* and *Polypodium polypodioides* var. *michauxiana* (*Schuster* 29043, 28809, 29060); upper falls, Whitewater R., Jackson Co. (*Anderson* 8747! *Schuster* 40567); Rocks in canyon of lower course of Dark Ridge Creek, near Balsam (*Andrews* 274! in herb. Y as *P. ludoviciana;* a delicate, green phase with moderate to barely bulging trigones); intermittently damp rocks by waterfall, above Linville Caverns, McDowell Co. (*Schuster* 40351, 40367, 40372; with *Anomodon, Radula complanata, R. andicola, Metzgeria conjugata, Lejeunea laetevirens*). Calcareous rock-face above falls of Crow Creek, Cullasaja Valley between Highlands and Franklin, Macon Co. (*Schuster* 40856; a small, virtually unbranched xeromorphic sun phase); on sandstone boulder, gorge of Pacolet River, near Tryon, Polk Co. (*Patterson* 2848!, 2845!; the former a

"normal" phase with small trigones, the latter a more brownish, xeromorphic phase approaching var. *caroliniana*). SOUTH CAROLINA: West branch of Estatoe River, in ravine, Pickens Co. (*Schuster* 37625, 37651b, 37625a, 37620b, 37669a, 37624a; the robust extreme of the species, freely producing gynoecia and propagula; in part approaching var. *caroliniana*); open S. end of gorge of Estatoe R., N. Pickens Co. (*Schuster* 37690a); transitional between the species and var. *caroliniana* is the collection from Whitewater R. Gorge, above Jocassee, Oconee Co. (*Schuster* 25108). TENNESSEE: Little America, near Island Home, Knox Co. (*Sharp* 34339, *male plants*); siliceous rock, Hickory Creek below Jellico, Campbell Co. (*Sharp* 3643; fragmentary, a mod. *parvifolia-subintegrifolia,* with median cells only 18-21 μ; possibly mesodermous phase of var. *caroliniana*); calcareous rock, Ladd's Cove, Bottle Creek, Marion Co. (*Sharp* 34956); calcareous bluff, near Jasper, Marion Co. (*Sharp* 34927 p. p. with *Radula complanata*); Bluff, left prong of Greenbrier, above 3000 ft., Sevier Co. (*Sharp* 3873; mixed with *P. sharpii* subsp. *sharpii;* cells small, the median 20-24 μ wide; postical leaf-base with longitudinal cell-walls thick; approaching var *caroliniana*). GEORGIA: Unicoi Gap, White Co., 2968 ft. (*Schuster* 25761, 25761a, 25761b). MISSISSIPPI: Tishomingo State Park, Tishomingo Co., *ca.* 750 ft., on subcalcareous sandstone (*Schuster* 19738, p. min. p., among *Frullania asagrayana* cf. *tamarisci*).

As is developed elsewhere, the report of this species from Washington, D.C. (Evans, 1896) is based on misdetermination of *P. yokogurensis* subsp. *fragilifolia.*

Ecology.—P. virginica appears to be typically a species of damp to dry limestone or sandstone ledges or cliffs. Although not uniformly associated with limestone ledges, the association is a marked one when one considers that in the Southern Appalachians calcareous outcrops are rare and local, yet more than half of the collections of *P. virginica* seen are cited as from calcareous rocks.

On calcareous boulders and cliffs, in partially exposed sites, common associates are *Radula complanata, R. andicola, Frullania squarrosa, F. plana, Porella platyphylla* and *platyphylloidea,* and with accumulation of a little soil, *Reboulia hemispherica,* as well as the mosses *Anomodon minor, A. attenuatus,* and *A. rostratus.* The *Plagiochila,* and associated bryophytes form dense mats, intermittently dry, in which such xerophytic ferns as *Asplenium resiliens* and *Polypodium polypodioides* undergo ecesis (in *Schuster* 28809, 29043, 29060; Linville Caverns, N.C.). Similarly, on calcareous bluffs (*Sharp* 34927; near Jasper, Marion Co.) the liverwort *Radula complanata* and mosses *Anomodon attenuatus, A. rostratus* and *Taxiphyllum geophyllum* are associated. At both of these sites, where conditions verging on the xeric pertain, the *Plagiochila* occurred as a large-celled, nearly leptodermous phase. This is the phase from which the species was described, from limestone at the entrance to a cave.

P. virginica also occurs on large and medium-sized, noncalcareous boulders, lying in relatively open Oak-Hickory forest (as at Unicoi Gap, Georgia; *Schuster* 25761 *and* 25761a, b). The associated hepatics at this site were *Frullania plana, Porella platyphylloidea, Metzgeria crassipilis,* and *Radula complanata.* The plants, from this site, from an unusually xeric habitat, possessed slightly to moderately bulging tri-

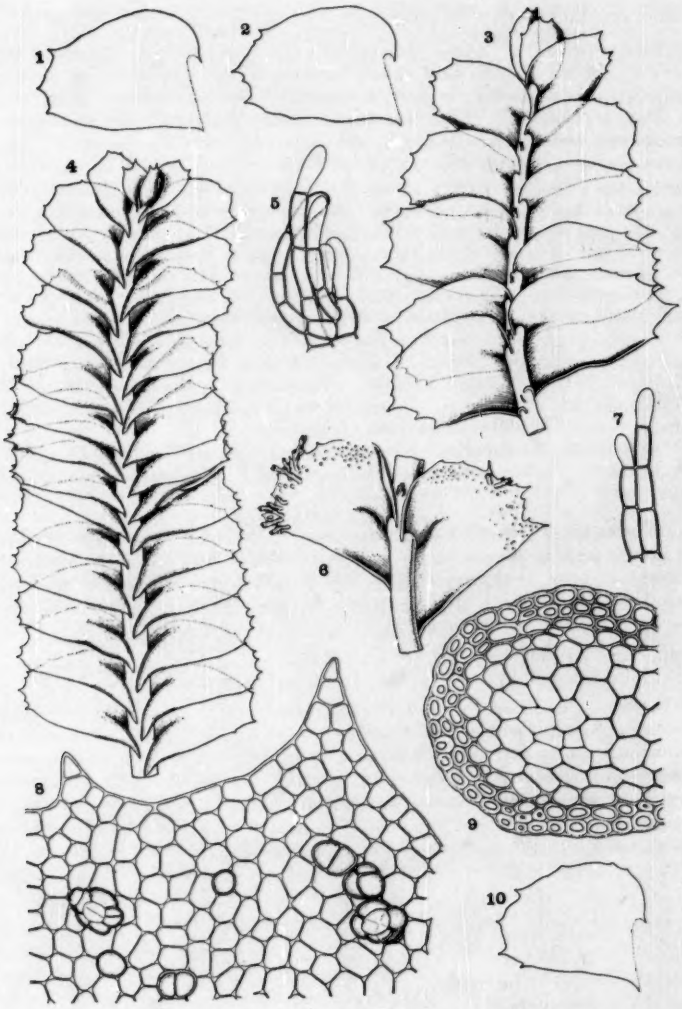

Fig. 44.—*Plagiochila virginica* Evs., typical. 1-2. Leaves (x 16); 3. Large shoot, postical aspect (x 13.5); 4. Shoot, antical aspect (x 12); 5. Relatively large underleaf (x 220); 6. Postical aspect of shoot-sector with propagula (x 13); 7. Underleaf (x 280); 8. Cells of leaf-apex, with young propagula (x 215); 9. Stem cross-section (x 175); 10. Leaf (x 13). (Figs. 1-5, 7-10, from plants collected at Unicoi Gap, Georgia, *Schuster;* for oil-bodies see Fig. 60:8; fig. 6, Linville Caverns, N.C., *Schuster* 29043.)

gones, but lacked the confluent trigones of the postical leaf-base. Other collections from "on rocks in woods" and from "sandstone boulders in woods" have been seen. The species is also common on boulders and ledges in rich Oak-Hickory forest at Tishomingo State Park, Mississippi (*Schuster* 19738), over sandstone rock-walls, associated with xerophytes such as *Frullania asagrayana*, cf. *tamarisci*, *Porella pinnata*, *Polypodium polypodioides*, etc. Such xerophytic and meso-xerophytic occurrences appear to be much commoner than the few cases where the species has been found on "moist rocks, at base of gorge" or "moist limestone cliffs."

The marked frequency on, if not obligate restriction to, limestone rocks, and the ability to tolerate relatively xeric conditions are the two most marked features of typical *P. virginica*. There is an almost constant association with *Anomodon*, although the species occasionally occurs on damper, noncalcareous ledges, associated with *Metzgeria hamata* and *Lejeunea laetevirens* (*Schuster* 40567). When occurring under such mesic conditions, the separation from var. *caroliniana* becomes critical.

The type material of the species appears to be a very atypical phase (mod. *parvifolia-viridis-leptoderma*) only 1-2 mm wide (Evans, 1892), in which the dentition of the leaves is hardly normally developed, and in which the broadly ovate leaf shape is not fully realized (Fig. 43:1-4); there are fewer teeth than normal ("varying in number from 2 to 3 on each leaf, usually 4 or 5"); the aerial shoots are normally simple. The plants are also abnormal in lacking propagula, which typically are abundantly produced.

By contrast, the ramified, robust plants from South Carolina (*Schuster* 37625) are up to 4-5 mm wide, and apparently represent the mature state of the species. These plants occurred in abundance on the vertical faces of dry but deeply shaded, large boulders and ledges, which were at least weakly calcareous, associated with *Porella platyphylloidea*, *Porella pinnata* subsp. (an undescribed subspecies!), *Cololejeunea ornata*, *C. biddlecomiae*, *Radula andicola*, *R. obconica*, *Lejeunea laetevirens* and *Metzgeria conjugata* and *myriopoda*. The plants had smaller, blunter and shorter teeth of the leaves, but these were usually more freely developed, usually 4-7 per leaf, but in some cases the leaves were subentire except for two weak teeth at the subtruncate apex.

Differentiation.—The primary characteristics of this species are (a) the contiguous to moderately imbricate, usually ovate leaves, which (b) freely produce propagula on the postical, but never on the antical faces; (c) the leaves short-decurrent postically, leaving the stem typically extensively exposed; (d) the very small to ephemeral underleaves; (e) the widely spreading leaves; (f) the sparing branching, but with the ultimate branches of at least mature plants furcate and terminal in origin. The species is variable and the weak phases of extremely shaded conditions (mod. *parvifolia*) are particularly difficult to comprehend. No regional species of *Plagiochila* has been more misunderstood. Indeed, the many collections seen had all been assigned to other species (*P. sullivantii*, *P. ludoviciana*) and the only collection,

other than the type, which has been assigned to the species (Evans, 1896) represents still another species, *P. yokogurensis*.

In spite of having been widely confused with *P. ludoviciana* and *P. sullivantii*, *P. virginica* bears only the most general and superficial relationships to these species.

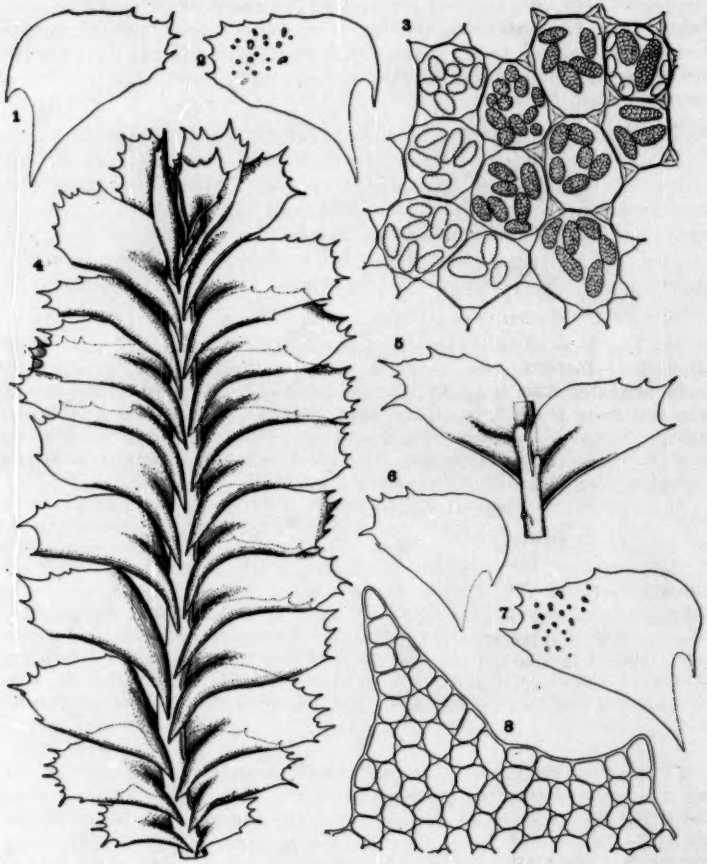

Fig. 45.—*Plagiochila virginica* Evs., robust phase with aerial branching, transitional to *P. v. caroliniana*. 1. Leaf (x 12); 2. Leaf, postical aspect, with propagula (x 12); 3. Median cells with oil-bodies (x 516); 4. Apex of mature shoot (x 15); 5. Shoot-sector, postical view (x 16.5); 6. Leaf (x 12); 7. Leaf, with propagula, postical aspect (x 17); 8. Cells near leaf-apex (x 212). (Figs. 2-4, 7-8 drawn from plants from Whitewater R., S. C., *Schuster* 25108; figs. 1, 5-6 from *Anderson* 10338, N.C.; bracts and perianth of this type illustrated in Fig. 46:9-11.)

Although the plant agrees with *P. sullivantii* in the approximate angle (55-76°) at which the horizontal leaves spread from the stem-apex, as well as in the approximate cell-size and cell-type, and in the few but often sharp marginal teeth of the leaves, there are numerous characteristics separating the two. Therefore, the statement by Frye and Clark (*loc cit.*, p. 440), in which doubt is expressed as to the distinctness of *P. sullivantii* from *P. virginica* can only be interpreted as indicating a lack of comprehension of these taxa. *P. virginica* differs from *sullivantii* not only in the constantly green color and the dull texture, but in the mode of asexual reproduction (*via* propagula of the persistent leaves), in the relatively numerous oil-bodies per median cell, and in the basic leaf-shape (ovate to ovate-rectangular, vs. obovate). Any close relationship between the two is quite unthinkable.

Although the species bears certain similarities to *P. ludoviciana* (basic leaf-shape, dentition, leaf-proportions, mode of asexual propagation, etc.), it differs from this species in several significant features: in the much less closely imbricate leaves (with the stem, in postical aspect, widely exposed); in the short-decurrent postical leaf-bases, which are not at all squarrose or reflexed; in the smaller size of the plant; and in the minute underleaves. Only rarely are obvious, laciniform underleaves present.

P. virginica also bears certain superficial similarities to, but is not closely related with *P. columbiana*. It was keyed out with this in Evans (1896). The much smaller leaf-cells at once separate *P. virginica* from *P. columbiana* (which agrees with *P. arctica* in having the largest cells of all our species, averaging *ca.* 38-42 μ in the leaf-middle, occasionally more). *P. virginica* also differs from *P. columbiana* in having more distinctly ovate, more elongate leaves (at least 1.2-1.5 $\times$ as long as wide, even on juvenile leaves), and apparently in never showing well-developed underleaves.

Most underleaves are very small in *P. columbiana*, but as Evans points out, a few are large and lanceolate. Such underleaves are quite unknown in *P. virginica*. Frye and Clark attempted to separate *P. virginica* on the basis of "underleaves wanting," which Evans also indicated to be the case in his original diagnosis. However, an isotype of *P. virginica* shows occasional underleaves, consisting of 1-2 uniseriate filaments 2-4 cells long, each tipped with a hyaline slime-papilla; much of the other material seen had obvious underleaves. No separation appears possible on that basis. Furthermore, the Unicoi Gap material is clearly provided with underleaves. The most important character differentiating *P. virginica* is the ability of the species to produce propagula (which *P. columbiana* is quite unable to form). Any close relationship between these two species is improbable.

The poorly developed type material also shows relatively slight dilation of the postical leaf-bases, with portions of the postical margin, in extreme cases, nearly parallel to the antical margin. Such plants, furthermore, often have only 1-2 teeth on the postical margin, while the apex is sharply bidentate or almost bilobed (Fig. 43:1-4); such plants could give rise to confusion with *P. austini*, and might be regarded as a deviant, atypical form of the latter. However, the broader leaf-form, the total lack of caducous leaves, the green color, and the abundant reproduction by leafy propagula, as well as the ovate

leaf-form of well-developed plants and the dull texture prohibit confusion.

In addition to confusion in the literature (and in herbaria) with the preceding species, the writer has also seen material of *P. yokogurensis* subsp. *fragilifolia* misdetermined as *P. virginica*. However, *P. virginica* differs in several important respects from *P. yokogurensis*, among them: the dull texture when dry; the antically shorter decurrent leaves, which are never conspicuously falcate; the persistent distal portions of the leaves. Dry plants are separable at a glance because of the very different texture.

Although there has been confusion in the American literature bebetween *P. virginica* and the preceding four species (*P. sullivantii, P. ludoviciana, P. austini, P. yokogurensis*), there is no immediate relationship with them. The species has been so consistently misunderstood in the American literature that no one has been able to obtain any accurate idea of what the name *P. virginica* actually meant. Indeed, its author shortly after proposing it confused the plant with the unrelated *P. yokogurensis!* Most of this difficulty originated in the fact that the type plants of *P. virginica* are so impoverished and ill-developed that only prolonged study of a long suite of specimens made it possible to demonstrate that the type plants were conspecific with the much more robust material here referred to it. As soon as this conspecificity was established, it became clear that the affinity of *P. virginica* was directly with the Mexican (and supposedly also West Indian) *P. contigua* Gottsche (1863, p. 30, pl. 14). Indeed, the writer is not yet convinced that *P. virginica* can be maintained as a distinct species, but may represent a mere Appalachian race of *P. contigua*. Until fresh material of the latter, from Mexico, becomes available, the two are maintained as distinct.

The two taxa agree in the virtual lack of underleaves (Gottsche fails to show them in his carefully executed figures; Evans specifically states "amphigastria none"), although it must be assumed that the obsolescent underleaves were overlooked by both workers. They also agree in the angle of orientation of the leaves; the leaf shape; their weakly imbricate orientation; the dentition of the leaves, and particularly the tendency for the leaves to be subtruncate at the apex; in the juvenile perianth with a weak and low antical wing of the basal half of the keel; the irregularly ciliate-dentate perianth mouth, and the shape of the bracts. Only three slight differences suggest that two distinct taxa are at hand: (a) the bracts in *P. contigua* are more fully and regularly serrate-dentate, with the teeth *ca.* 20-26 teeth per bract; (b) the perianth-mouth, judging from Gottsche's drawing, bears narrower and more acuminate teeth; (c) the vegetative leaves tend to have the postical margin more freely dentate, often with 2-8 teeth. In *P. virginica*, well-developed plants often have only 2-5 teeth of the whole leaf, of which only 1-2 occur on the distal half of the postical margin. However, this is not always the case (Figs. 46:4, 45: 1-2, 4). In view of the demonstrated great variation in *degree* of dentition of perianth-mouth, leaves and bracts in *P. ludoviciana* the claims of *P. virginica* for recognition as a species remain very weak indeed.

In addition to the very close affinity to *P. contigua, P. virginica* also appears directly related to another Mexican species, *P. xalapensis* Gottsche, a species with more decurrent antical leaf bases, and sharper, stronger dentition. More distantly allied are *P. subconvoluta* Gottsche, a species with almost perfectly oblong ♀ bracts and a more finely ciliate-dentate perianth-mouth, and probably also *P. muelleriana* Gottsche, also a species with a more closely, finely and freely ciliate perianth-mouth.

Variation.—Since this species was described from a leptodermous completely atypical extreme, the range of variation of the species is difficult to comprehend. The writer, at first, was of the opinion that *P. virginica* could represent juvenile material of several species, and therefore should be dropped as a *nomen dubium,* but now believes that the Unicoi Gap plants, those from South Carolina, and those from Linville Caverns, North Carolina, treated below, may well represent the typical form of this species. Collections in West Virginia, from near the type station, are needed to confirm this hypothesis. The Ammons work on West Virginia hepaticae (in which *P. virginica* is mentioned only among the excluded species) does not help at all in indicating the identity of *P. virginica.* The writer therefore suggests that, for the present, the materials collected by the writer in South Carolina, at Linville Caverns, North Carolina, and at Unicoi Gap, Georgia, and the plants collected in Giles County, Virginia, by the writer and by Patterson, be considered as "typical" of the species.

The species varies from a leptodermous extreme (type material; probably from an unusually moist site) to moderately pachydermous, with relatively small or moderate trigones, that may be moderately bulging (North Carolina, South Carolina, and Georgia plants). The most pachydermous type seen, represented by plants from Virginia (near Hot Springs, on limestone near stream, The Cascades, Bath Co.; *Patterson* 1448) has the trigones rather obviously bulging in most cases, with the longitudinal walls of median and basal cells sometimes evenly thick-walled. These plants are unusually robust (up to 4 mm wide), show an occasional dichotomization of the leafy aerial shoot system, and possess no propagula; they form a close approach to *P. virginica* var. *caroliniana,* but are still clearly *P. virginica.* Identical with these plants are those from South Carolina (Fig. 45, 46:9-11). The ability to develop trigones appears to require a relatively intense stimulus, in this taxon (compared to the related *P. virginica* var. *caroliniana*). In the Linville Caverns plants (*Schuster* 29043), for instance, the trigones are concave-sided and small: yet the plants grew under xeric conditions, near the crest of a cliff, in partial sun, associated with such xerophytic Hepaticae as *Radula complanata* and *Frullania squarrosa* (as well as xerophytic ferns, *Asplenium resiliens* and *Polypodium polypodioides* var. *michauxiana*). In the Georgia plants, from even more xeric sites (see section on Ecology), the trigones were barely bulging. One of the peculiarities of the typical species, therefore, is the inability to develop coarse, confluent trigones; the species thus exists chiefly as the mod. *leptoderma* and *mesoderma.*

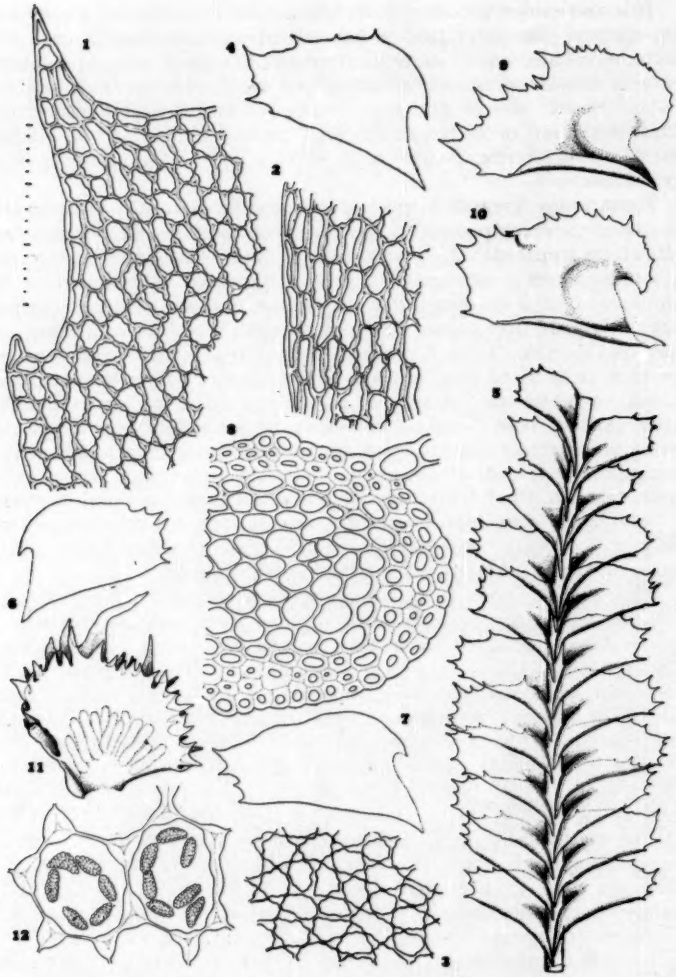

Fig. 46.—*Plagiochila virginica* var. *caroliniana* Schuster and transitional material to typical *virginica* (figs. 9-11). 1. Cells of leaf-apex (x 165); 2. Cells near postical base of leaf (x 165); 3. Median cells (x 165); 4, 6-7. Typical leaves (x 16); 5. Shoot (x 9); 8. Cross-section of stem (x 220); 9-11. Bracts and juvenile perianth, from one gynoecium, of form transitional to typical *virginica* (9-10, x 16; 11, x 33); 12. Median cells with oil-bodies (x 590). (Figs. 1-8 from *Anderson* 10338, Cullasaja Falls, N.C.; 9-11, from *Schuster* 25108, Whitewater R., S.C. [see also in Fig. 45]; 12, from *Schuster and Sharp* 34620, Blount Co., Tennessee.)

It is also evident, from the rather limited collections, that the plants are nearly always green, only the stems becoming brownish; the plants thus almost constantly are a mod. *viridis*. In general the dentition is not exceedingly coarse. The species appears unable to produce a narrow-leaved extreme, or mod. *angustifolia*. All plants seen were slightly imbricate-leaved or approximate-leaved, and had rather broad leaves. The range of modification, in this regard, therefore, is less than in var. *caroliniana*.

Perhaps the greatest degree of variation in this species occurs in the extent to which propagula are formed. In the type (probably from a mesic environment) no propagula are developed; in the xeric phase (Linville Caverns) we find that there is luxurious and abundant development of filiform propagula. As in *P. ludoviciana*, propagula production appears to be stimulated by increased difficulty in water uptake, and by more xeric conditions in general. This, present observations indicate, is the reverse of the situation in *P. virginica* var. *caroliniana*, in which propagula are frequent in the large phase from damp, shaded rocks (mod. *latifolia-viridis-mesoderma*), while the typical xeric extremes (mod. *augustifolia-colorata-pachyderma*) are almost or quite devoid of propagula.

The best developed material of the species which I have seen are the 4-5 mm wide plants from the Estatoe R. Ravine in South Carolina (*Schuster* 36625) and from the Whitewater R. Gorge in South Carolina (*Schuster* 25108). In both of these collections there are numerous gynoecia. Furthermore, they show an identical branching system as in *P. dubia:* the aerial shoots are produced as intercalary lateral branches from a creeping, more or less small-leaved rhizomatous system. Each aerial shoot may develop 1 or 2 monopodial, widely spreading, lateral intercalary branches, but eventually forks pseudodichotomously, the forks commonly becoming unequal in length, with at least one again forking, the branches being uniformly terminal. The ultimate branches, which are thus pseudodichotomously oriented, may be short (2-3 leaf-pairs) or elongated (6-12 leaf-pairs) before producing gynoecia. The gynoecia invariably produce a single subfloral innovation, which may remain sterile or may soon end in another gynoecium. In no case could gynoecia without subfloral innovations be found, or gynoecia with paired innovations (differing thus from *P. dubia*). Branching of the aerial shoot system is rare and sporadic, however, except in such robust female plants.

The copiously developed plants from South Carolina (referred to above) show a close and unmistakable similarity to *P. contigua* G. They agree in basic size, the form, dentition, and orientation of the leaves, and in the form of the immature perianth.

The preceding, leptodermous to mesodermous plants are very largely restricted to calcareous sites. Away from calcareous sites typical *P. virginica* is often supplanted by an xeromorphic type:

Plagiochila virginica var. **caroliniana** var. n.
Figs. 46:1-8, 12; 47

P. virginicae typicae similis; differt: planta minima, pauciramosus, olivacea, sicca plus minus brunnea; foliis angustius ovatis vel ovatis-rectangulatis; cellulae basales parietibus ± aequaliter incrassatis; cellulae apicales vel mediae ca. (16-

19) 18-21 (24) μ x 18-24 (26-30) μ, trigonis maximis, nodulosis. Typus: Bearwallow Creek, Toxaway Gorge, SW. of Rosman, North Carolina (*Anderson* 12823).

Plants green, with stems rigid and brownish, or the entire plant brownish (the *cell-walls of the leaves becoming quite yellowish*). Shoots usually ± dichotomously branched, (1.8) 2.5-3.5 mm wide usually. Stems rigid, *ca.* (130-180) 200-235 μ wide, with cortex strongly pachydermous, well-defined; dorsal and ventral cortical cells similar, bast-like, thick-walled, 10-12.5 μ in diameter x 42-75 (85) μ long; cortical cells in (2) 3-4 layers, rigid; medulla in 5-8 layers, the cells (14) 16-20 (24) μ in diameter, slightly collenchymatous; stem as a whole 12-16 cells high. Leaves distant to weakly imbricate, varying

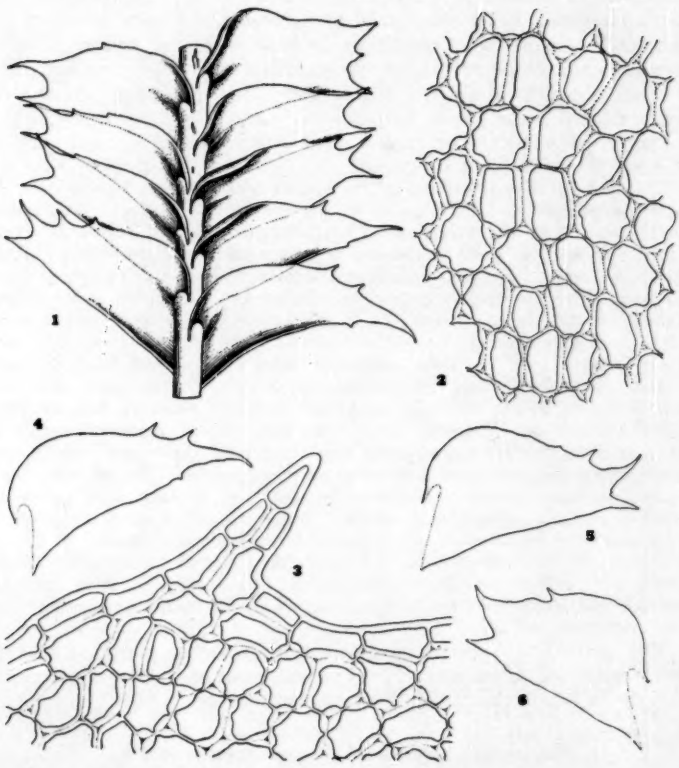

Fig. 47.—*Plagiochila virginica* var. *caroliniana* Schuster. 1. Shoot-sector, postical view (x 31); 2. Median leaf cells (x 400); 3. Cells of postical leaf-margin, above middle (x 400); 4-6 Leaves (x 31). (All from xeric, brown mod. *colorata-pachyderma-angustifolia*, from *Anderson* 8660.)

from rather broadly ovate (identical with those of typical *virginica;* up to 1350 μ wide x 1800 μ long) to *narrowly ovate-falcate* (then only 400-500 (650) μ wide x 800-1000 μ long, *averaging up to twice as long as wide*). Cells *strongly collenchymatous,* often with yellowish walls; cells along leaf-margins, *even near leaf apex, tending to be strongly* elongated in 1-2 rows; subapical and median cells tending to be smaller than in typical *P. virginica, ca.* (16-19) 18-21(24) μ wide x 18-24(26-30) μ long; cells along postical margin near middle of leaf *ca.* 13-16 (21) μ wide x 23-28 (36) μ long, those within margin nearly isodiametric and 17-21 (24) x 18-22 (25) μ long; cells at postical base becoming narrower and more prominently elongated; cell-walls of marginal 1-3 cell-rows *tending to become strongly and equally thick-walled,* near the postical leaf-base the marginal 3-6 cell rows similarly, strongly longitudinally thick-walled, the *cell lumens becoming nearly linear;* subapical, median and basal interior cells with coarse trigones, *those of leaf-middle and base tending to have the trigones strongly longitudinally confluent.* Oil-bodies mostly (2-3) 4-8 per cell and 4 x 6.5-8 μ, a few to 5 x 12 μ; in some cells 10-11 oil-bodies which are only 3-4 μ and spherical 3.5-4 x 5-6.5 μ; oil-bodies papillose-segmented; chloroplasts *ca.* 4 μ. Underleaves vestigial.

Female plants (2) 3-4 times dichotomously furcate, the gynoecia terminal on the ultimate branches, usually with innovations. Bracts similar to leaves, suberect to erect, the apices spreading, postical margin undulate, ovate-oblong, ampliate, *ca.* 1400-1500 μ long x 1150-1225 μ wide (the width difficult to accurately determine, due to the strongly postically involute antical margin); postical margin and apex very irregularly and coarsely dentate with broad-based, scarcely acute or subacute teeth (*ca.* 16-20 teeth per bract); the antical margin of bract entire. Juvenile perianth (*ca.* 900 μ wide at mouth) with short antical keel, unwinged, except above base and shorter, unwinged postical keel; transverse and truncate-rounded mouth closely and irregularly dentate with subacute to blunt, to angulate, broad-based teeth (teeth commonly 4-6 cells wide at base x 6-8 cells long), and with a few longer laciniae (10-12 cells wide at base x 20-30 cells long); cells of teeth essentially isodiametric.

Type.—Moist rocks, edge of stream, in shade, Bearwallow Creek, Toxaway Gorge, SW. of Rosman, North Carolina, 1100 ft. (*Anderson* 12823); in herb. Duke University; schizotype in author's herbarium.

Distribution.—*P. virginica caroliniana* appears to have a highly restricted distribution, at median elevations in the Southern Appalachians, at from 1050 ft. to *ca.* 3200 ft.

VIRGINIA: Sink Hole near Lucas Memorial Church, near Pembroke, Giles Co. (*Patterson,* July 1943!; listed by Patterson as *P. ludoviciana;* plants with relatively small trigones, grading into *P. virginica,* typical); near Big Cascades, on side of siliceous boulder, 3000 ft., Mountain Lake, Giles Co. (*Sharp V-47*; listed by Sharp, 1944, as *P. ludoviciana*). TENNESSEE: Lower Roaring Fork, above Gatlinburg, Sevier Co., 1700 ft. (*Sharp* 35265!, 1935; listed as *P. ludoviciana* in Sharp, 1939); Greenbrier Cove, at Porters Creek, *ca.* 2500 ft.,

Sevier Co. (*Patterson, July, 1947,* as *P. ludoviciana;* with *P. austini!*); above the Orchard, Mt. LeConte, Sevier Co., 2800 ft. (*Sharp* 3577); siliceous Boulder, Meigs Creek, Sevier Co., 2000 ft. (*Sharp* 36219); Greenbrier Pinnacle trail, Sevier Co., 2800 ft. (*Sharp* 341093) (the preceding Sharp collections all cited in Sharp (1939) as *P. ludoviciana*); shaded moist holes in bluff, along Little R. above Forks, towards Elkmont, Sevier Co., 1800 ft. (*Sharp* 515!); below Tremont, *ca.* 1600 ft., Blount Co. (*Schuster* and *Sharp* 34620). NORTH CAROLINA: Upper Falls, Whitewater R., Jackson Co. (*Anderson* 8660!; *Schuster* 25052*; p.p.,* with *P. sharpii sharpii*); below Cullasaja Falls, 9 mi. N. of Highlands, Macon Co. (*Anderson* 10388!); Bearwallow Falls, Toxaway Gorge, Transylvania Co. (*Anderson* 6660!); Crow Creek, Little Fishhawk Mt., NW. of Highlands, Macon Co. 3700 ft. (*Anderson* 7940! *c. per. juv.*); W. side of Whitewater R. gorge *ca.* 1/6 mi. below High Falls, Jackson Co. (*Schuster* 34731, 34737, 34736); underside of deep recess at one side of High Falls of Whitewater R., *ca.* 2800 ft., Jackson Co. (*Schuster, L. E. Anderson, W. D. Billings* 34730) (Cotype); below High Falls, Whitewater Gorge, Jackson Co. (*Schuster* 40568, 25052); east of Rich Mountain, on Mull Creek just above juncture with Beachflat Creek, *ca.* 2500 ft., Jackson Co. (*Schuster* 39684 *p.p.,* with *Radula obconica*); Cullasaja Gorge, NW. of Highlands, Macon Co. (*Sharp* 141!; in herb. Y as *P. ludoviciana;* a somewhat brownish phase, very typical, with narrow leaves; admixed with *Radula andicola*); rocks of stream, side of Grandfather Mt., below Yonahlossa Road (*Andrews* 53!; in herb. Y as *P. ludoviciana*). Possibly referable to var. *caroliniana* are the robust fertile plants from SOUTH CAROLINA: *Ca.* 0.5 mi. below Lower Falls, Whitewater R., north of Jocassee, Oconee Co. (*Schuster* 25108; *c. per. juv.!;* transitional to typical *P. virginica*).

Ecology.—A taxon restricted evidently to damp, shaded, humid gorges and the rocky banks of shaded streams; usually restricted to acidic rocks (unlike typical *P. virginica*). The mesic habitat is characteristic. In several stations occurring with *Mnium carolinianum, Jubula pennsylvanica, Metzgeria conjugata,* and (nearby) *Dumortiera nepalensis* and *hirsuta,* and the filmy fern, *Trichomanis petersii.* Elsewhere found admixed, or in juxtaposition to *Plagiochila yokogurensis fragilifolia* and *P. austini;* occasionally on damp, shaded rocks associated with *Radula obconica* and *Fissidens* sp.

The strongly xeromorphic structure, with bast-like cortical stem cells, and strongly collenchymatous leaf-cells, *in spite of the restriction to damp sites,* is remarkable. As we have seen under *P. virginica,* typical, the latter often is found on dry calcareous rocks, often relatively exposed, yet has a green color throughout, little-thickened cortical cells, and little-collenchymatous leaf cells. This suggests that two physiologically different taxa are at hand. Unfortunately, the different behavior patterns are not absolutely correlated with sharp morphological distinctions.

Variation.—This taxon appears to show considerable variation in robustness and color, correlated with the isolation and saturation-deficit of its habitat. Three types of plants are distinguishable, on the basis of the available material.

(1) Mod. *viridis-latifolia-megafolia-mesoderma vel pachyderma.*—In this form, the entire plant is greenish, although the stems may be brownish-green; the shoot is wide, (1) 2-4 × dichotomous, the leaves relatively imbricate and

strongly antically decurrent (and the plants thus acquire the facies of *P. ludoviciana*). The cell-walls of this phase bear distinct and bulging trigones, which are, however, relatively small and sharply defined, never becoming confluent; plants of this type freely bear propagula. This material is represented by the South Carolina specimens as well as by several others (Upper Falls, Whitewater R., Jackson Co., North Carolina, *Anderson* 8747, DU; east of Rich Mt., on Mull Creek, Jackson Co., *Schuster* 39684). The most luxuriant development of these plants shows free furcate branching. These plants are transitional to "normal" *P. virginica* (Figs. 45, 46:9-11), and should perhaps be referred to it.

(2) Mod. *colorata-angustifolia-pachyderma-propagulifera.*—This type is represented by brownish plants (leaves brownish-green, but stems reddish-brown), with coarse confluent trigones, somewhat yellowish in color; the leaves are at times narrower than usual, often merely approximate; the shoots are smaller, usually 2.5-3 mm wide. Plants of this type bear propagula very intermittently. This material is represented by specimens from North Carolina (below High Falls of Whitewater R., Jackson Co., *Schuster* 40568; and below Cullasaja Falls, 9 mi. N. of Highlands, Macon Co., *Anderson* 10338; DU). (Fig. 46:1-8, 12.)

(3) Mod. *colorata-parvifolia-angustifolia-pachyderma-epropagulifera.*—This represents the extreme xeric phase of the species (plants strongly brownish, particularly the stems; leaves small, and plant poorly developed, only 1.8-2 mm wide; propagula not at all produced; cells with trigones confluent, the more elongate cells usually with the trigones confluent on the longitudinal walls to a point where the *bursata*-type of cell is simulated). These plants bear no resemblance at all to *P. ludoviciana* or *virginica*, but are apt (because of size, distant and narrow leaves, somewhat shining brownish color) to be mistaken for *P. austini*. This third type of plant is represented by two collections from North Carolina (Bearwallow Falls, Toxaway Gorge, Transylvania Co., *Anderson* 6660; Duke; and Upper Falls, Whitewater R., Jackson Co., *Anderson* 8660). (Fig. 47.)

The plants of the extreme xeric type would scarcely be considered related to the mesic extreme (type 1), were it not for the presence of intermediate plants (type 2), which clearly bridge the gap. The recognition of this taxon is most easily achieved when plants of types 2 or 3 (*i.e.*, the more xeromorphic forms) are at hand. These plants, in their strong pigmentation, and excessively strongly collenchymatous cells, differ from all our other species (except the pachydermous extremes of *P. sharpii*). In none of our other species are the trigones so salient, so freely confluent, and in no other case is the extreme *bursata*-type of cell simulated. However, the marginal cells of several species show a tendency for the development of equally thickened longitudinal walls (*e.g.*, in *P. diffusa*). Confusion with these species is scarcely possible, because these species have strong thickening of the cell-walls confined to the marginal cells.

The plants of type 3 are also characterized by the partly extremely narrow leaves (*ca.* 400-500 μ wide x 800-1000 μ long; averaging twice as long as wide, often acuminate distally or sharply bilobed. Such phases, furthermore, have the marginal cells usually strongly elongate and thick-walled, thus forming a border (and in this respect simulating *P. diffusa*). The narrow leaf-form, in such plants, is further correlated with a lesser development of the postical base, which is only slightly dilated. The width of such xeromorphic plants usually does not exceed 1.8-2.1 mm. The combination of brown color, narrow (and sometimes scarcely approximate) leaves, and the small size all suggest the quite unrelated *P. austini*.

P. virginica var. *caroliniana*, as here circumscribed, may prove to be a composite taxon. The aerial shoots of the fertile plants of type 1 are quite regularly 2-4 × pseudodichotomously (less often more nearly monopodially) furcate, and bear juvenile perianths. In them there is no marked tendency for the trigones, which are sharply defined, to become confluent, except at the postical base. These plants have exceedingly small cells of the leaves; averaging on fully mature, fertile shoots only 16-19 x 18-22 (24) μ in the leaf-middle. These plants appear closely allied to the mod. *mesoderma* of typical *P. virginica*.

All the other collections seen are of plants that are sterile with virtually unbranched or rarely monopodially branched aerial shoots. They tend to have larger leaf-cells, averaging from 19-23 μ wide medially, and the cell-walls of the leaves manifest a strong tendency to become longitudinally confluent. This tendency is most strongly evident in the marginal and submarginal cells, from the apex to the leaf-base. These cells then become equally thick-walled. No such tendency whatsoever occurs in the South Carolina material (Fig. 45:3, 8), which is transitional to "normal" *P. virginica*. The larger-celled plants, with often confluent trigones, grade somewhat into typical *P. virginica*. Possibly some of them may prove to belong to that species, as mere xeromorphic manifestations. The exceedingly mesic habitat, and strongly collenchymatous cells, of the type plants of *caroliniana* make it impossible to explain these as a mere environmental modification, however.

Clearly, the variability of the *P. virginica-caroliniana* complex remains a subject needing careful field study and fuller collections than now available.

In the last several years I have alternately considered var. *caroliniana* as a mere modification, or a full-fledged species. The collections made under the High Falls of the Whitewater R., North Carolina (*Schuster* 40567, 40568) suggest that two species may be at hand. On more exposed rocks occurs a green, mesodermous phase, without confluent trigones of the basal half of the leaf; these plants show regularly 1-2 dichotomous forks of the aerial stems, and tend to form patches. By contrast, on the underside and vertical faces of undercut, humid ledges occurs a much smaller plant, whose creeping primary stems produce at intervals erect (or pendent), unbranched, short leafy axes; the leaves are coarser-toothed and fewer-toothed; the stems are more rigid and brown; the basal halves of the leaves have very largely confluent trigones and more elongate-appearing cells. The latter plants, typical var. *caroliniana*, grew within 16-20 ft. of typical *P. virginica*!

The separation of plants of the "extreme" *caroliniana* type from small phases of *P. sharpii* is sometimes impossible in the field, the two being identical in facies. A small collection of *P. sharpii* from Cullasaja Falls (*Schuster* 49737) is a case in point. The plants agreed with *caroliniana* in being short (8-12 mm high usually), slender (1.5-2.1 mm wide), brownish-tinged, and in growing diffusely, the creeping stolons producing unbranched, erect, leafy axes at considerable intervals. Under the microscope the marginal cells were collenchymatous, exactly as are the inner cells, and the vitta was hardly distinct — as is often the case with very weak phases of *P. sharpii*. However, the smaller cell size (subapically 16-18 μ wide), the sharply nodulose trigones, and in particular the homogeneous oil-bodies served to place the plants into *P. sharpii*.

Plagiochila virginica var. **euryphylla** var. n.
Fig. 48

P. virginicae typicae similis, praesertim ad virgas tenuis vel juvenilis, sed differt aspectu magis pellucido; foliis latissime dilatatis, late ovatis vel ovato-triangularibus (0.9-1.33:1), ad virgas robustas dense imbricatis; foliorum marginibus subintegris vel obscure dentatis; folii basi ventrali valde undulata, P. undatae simili. Typus: Windy Falls, Horsepasture R., Transylvania Co., North Carolina (*Anderson* 8480).

Plants rather robust for *P. virginica,* up to 3-4 mm wide x 1.5-3 cm long, the aerial shoots nearly simple. Weak shoots somewhat similar to *P. virginica,* but the robust ones with much broader, more dilated, broadly ovate leaves that are somewhat wavy or crisped and have broadly deflexed postical leaf-bases. Stems *ca.* 300 μ in diameter, green to light brownish, without rhizoids except rarely below. Leaves varying from broadly asymmetrically ovate and 1300-1320 μ long (from insertion) x 1400-1520 μ broad to 1400-1500 μ broad x 1450-1575 μ long (*length, on the smaller, more broad-leaved shoots ca.* 0.9-1.1 $\times$ *the width*); the larger leaves to 1500 μ wide x 2000 μ long (*length* 1.33 $\times$ *the width*) and more narrowly ovate; postical margins strongly arched, quite dilated above base, nearly straight distally; antical margin usually nearly straight; both antical and postical margins more or less *strongly deflexed, especially the postical base which is erect or often broadly recurved* (*the leaf, as a consequence,* normally rather strongly convex dorsally and *hollowed in postical aspect*); outer portions of postical margin often somewhat undulate or crisped; *leaf-margins subentire to paucidentate, the often broadly truncate apex* with at best a few obscure, low, often rounded teeth, under maximal conditions with 3-5 rather obscure apical and subapical teeth; *leaves strongly imbricate,* on older and more robust portions of shoots the dilated and shingled *leaf-bases often virtually or quite hiding stem.* Cells distinctly collenchymatous, the subapical *ca.* 21-24 μ, the median *ca.* 21-24 (25) x 24-28 (32-34) μ; *those of the very short-decurrent postical base hardly differentiated,* mostly only 1.3-1.8 $\times$ as long as broad, *ca.* 18-20 μ wide x 22-30 μ long, rather thick-walled, at least as regards longitudinal walls. Underleaves minute, of a few cilia tipped with hyaline papillae, disappearing with age. Asexual reproduction via propagula present, but rare and local.

Type.—Moist rock, below Windy Falls, Horsepasture River, near Cashiers, Transylvania Co., North Carolina, *ca.* 2000 ft. (*L. E. Anderson* 8480; Aug. 20, 1949). In herb. Duke; schizotype in herb. author.

Distribution.—Known only from the type collection. Probably endemic to the restricted escarpment region of the Southern Appalachians, and restricted to the Mixed Mesophytic Cove Forest Region, to which *Mnium carolinianum* is also endemic.

Differentiation.—A distinctive taxon, characterized by the dense, strongly ampliate, broadly ovate, paucidentate leaves, which are long-decurrent antically, but short decurrent postically. The broadly ovate-triangular and subentire leaves suggest a similarity to *P. undata.* This

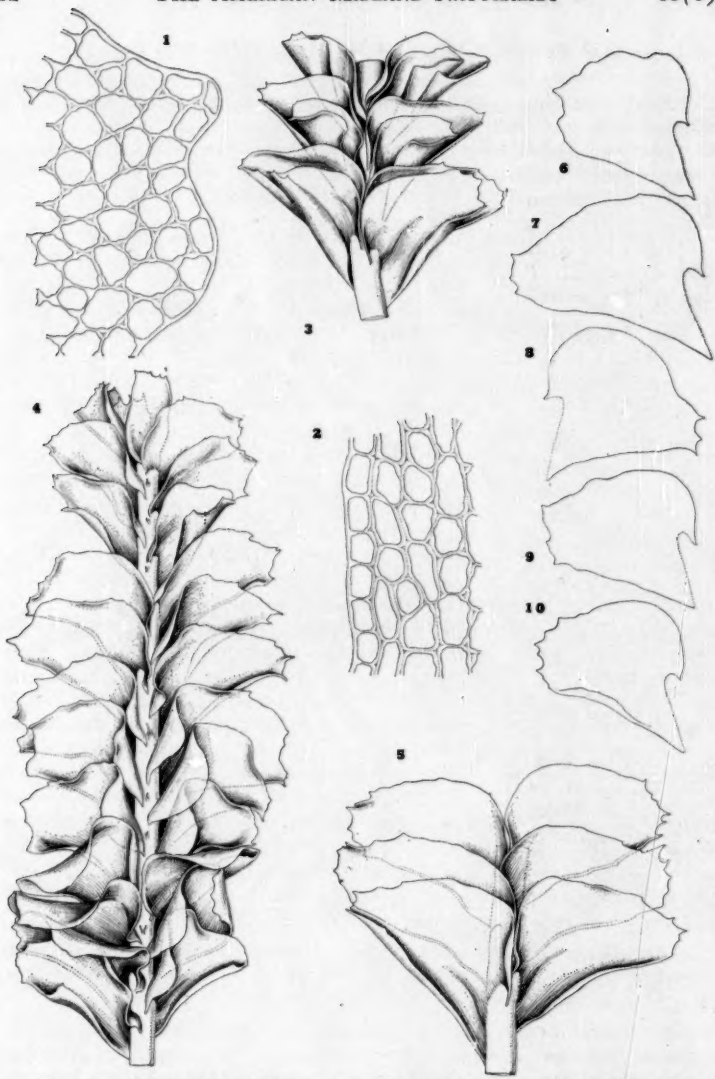

Fig. 48.—*Plagiochila virginica* var. *euryphylla* Schuster. 1. Cells of leaf-apex (x 232); 2. Cells of postical leaf-base (x 232); 3. Sector of dense-leaved extreme, postical aspect (x 12); 4. Typical shoot, postical aspect (x 12); 5. Robust shoot-sector, postical aspect, with approach to typical *P. virginica* (x 12); 6-10. Leaves (x 12.5; 6, 8-10 normal leaves of dense-leaved shoots; 7, leaf of robust extreme). (All drawn from type material, Horsepasture R., N.C., *Anderson*.)

similarity to *P. undata* is enhanced by the closely imbricate leaves, their strongly postically secund orientation when dry (an orientation which persists to some degree when the plants are moist, as a consequence of which they look strongly convex antically, strongly concave postically), and by the somewhat circinate coiling of the shoot-apex in drying. The postically secund leaves and the somewhat coiled or deflexed shoot-apices (when dry) also suggest *P. hypnoides,* a species which also agrees in the short decurrent, imbricate, postical leaf-bases.

These similarities to *P. undata* and *P. hypnoides,* however, are quite superficial. *P. virginica euryphylla* differs at once from *P. undata* in the short-decurrent postical leaf-bases, and in the minute underleaves, as well as in the much less markedly undulate postical leaf-margins. The broadly ovate leaf-shape, the reduction of the dentition, and the obsolete underleaves at once separate the species from *P. hypnoides.*

The relationships of *P. virginica euryphylla* are with the Contiguae, rather than with the Hypnoides and Crispatae. These relationships to the Contiguae are indicated by (a) vestigial underleaves; (b) cell size and bulging trigones; (c) rather weak dentition, absent near the postical leaf-bases; (d) ovate leaf form; (e) segmented oil-bodies; (f) very short-decurrent postical leaf-base; (g) presence of propagula on the postical leaf-faces.

Among the Contiguae, *P. virginica euryphylla* appears to be related most immediately to the *P. virginica-caroliniana* complex. The shorter and broader, postically more ampliate leaves, the denser insertion of the leaves, and particularly the similarity in facies of mature plants to *P. undata* separate *P. virginica euryphylla* from the immediate vicinity of other members of this complex. In none of the numerous collections of the *P. virginica-caroliniana* complex seen was there an equally marked tendency for the teeth of the leaves to become obsolete as in var. *euryphylla.* A more distant relationship may occur with the two Mexican species, *P. stolonifera* and *P. anomala* L. & G. *P. virginica euryphylla* has a leaf-shape which closely approaches that of these two species. As in *P. anomala,* some leaves are entire and obtusely pointed at the apex; as in *P. stolonifera,* other leaves bear a few teeth distally. In some respects, *P. virginica euryphylla* falls midway between these two Mexican species in respect to the leaf-shape. However, the leaf-cells of *P. anomala* are very different, according to Gottsche (1863), and the dentition of the leaves in *P. stolonifera* is more copious, extending to near the postical leaf-bases. The absence of comparative material of these two taxa makes a further comparison useless. It should be noted, however, that Stephani (1905, p. 596) transferred *P. anomala* to *Syzigiella.* Stephani also described the cells of *P. stolonifera* as very strongly collenchymatous, eliminating that species from further consideration.

The mature shoots of this taxon are so very different in facies from any form of *P. virginica* which I have seen that originally the plants of the present variety were considered to be a distinct species. However, less well-developed plants show a strong similarity to *P. virginica*

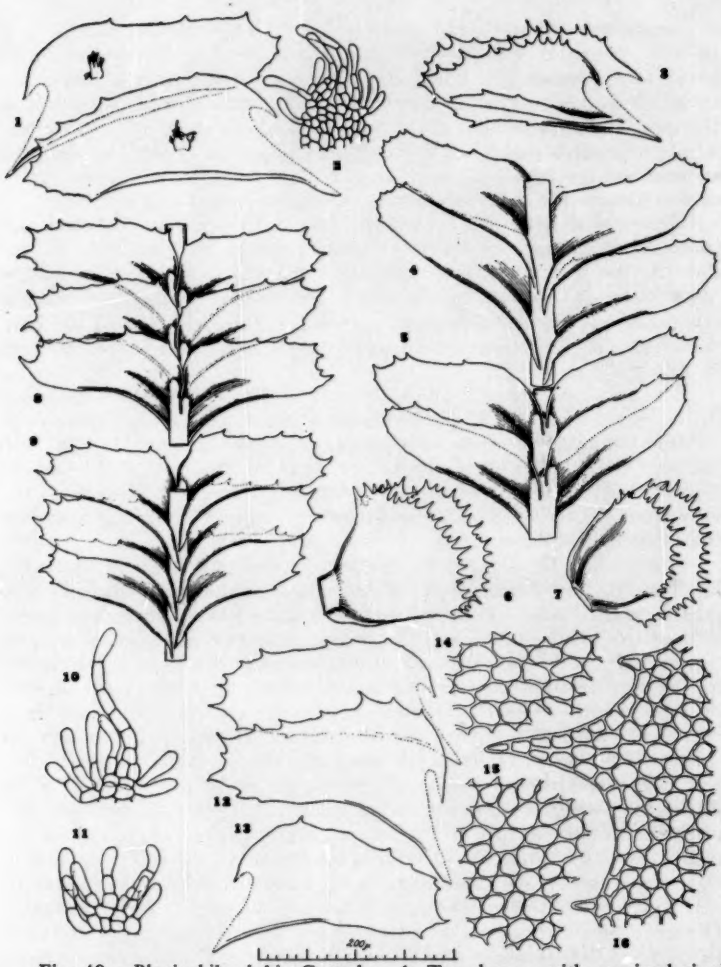

Fig. 49.—*Plagiochila dubia* Gottsche. 1. Two leaves, with maximal sized underleaves drawn to same scale (x 18); 2. Large underleaf (x 78); 3. Female bracts, immature in size (x 18); 4. Shoot-sector of robust plant, antical aspect (x 12.5); 5. Same, postical aspect (x 12.5); 6-7. Juvenile perianths in lateral view (x 18); 8-9. Shoot-sectors of coarsely dentate phase, postical and antical aspects (x 12.5); 10-11. Normal underleaves (x 142); 12-13. Leaves (x 18); 14. Cells below leaf-apex (x 142); 15. Cells near leaf-middle (x 142); 16. Cells of leaf-apex (x 142). (Figs. 1, 3, 6-7, 12-13 drawn to one scale; figs. 4-5, 8-9 drawn to one scale; figs. 10-11, 14-16 drawn to scale at bottom of plate; figs. 1-7 from *Schuster* 33475a, Devil's Millhopper, Florida; 8-16, *Schuster* 33537, Alum Bluff, Florida.)

var. *caroliniana*. Until more copious collections of var. *euryphylla* are found, it seems best to give it only varietal rank.

As is noted elsewhere, *P. virginica* as delimited here is now an extremely polymorphous taxon and may well prove to embrace two or more species when the variability of its members is studied experimentally. It is possible that the unique development of the present plants is in part influenced by anomalous environmental conditions. Whatever the future status of the plants, the included plate clearly shows the differences they exhibit, as contrasted with *P. v. virginica* and *P. virginica caroliniana*.

PLAGIOCHILA DUBIA Lindenb. et Gottsche
Figs. 49-52; 53:6-8

Plagiochila dubia Lindenb. et Gottsche, *in* G. L. et N., Syn. Hep., 630, 1847; Gottsche, Mex. Leverm. 16, Pl. II, figs. 1-8, 1863.
Plagiochila floridana and *P. austini*, in part, of certain American authors.

Plants pure to somewhat olive-green, the stems ± olive-brown to brown, *dull*, typically forming loosely prostrate patches, on trees or on rocks, the leafy shoots ascending or arching away from substrate, simple or *loosely pseudodichotomously furcate;* branches widely spreading; gynoecia usually with 2, less often with 1, subfloral innovations (which may again be swiftly floriferous, and again bear innovations, leading occasionally to the formation of dendroid branch-systems at the apices of female branches). Main shoots varying from 3.2-4.2 mm wide (on xeromorphic extremes, and in plants from the periphery of the range sometimes only 2.0-3.2 mm wide); stems slender, (190-200) 240-275 μ in diameter. Rhizoids very few. *Leaves when moist contiguous to slightly imbricate,* occasionally moderately imbricate, in drying deflexed, *somewhat convolute-twisted, and appearing quite remote,* quite linear, when moist *erect-spreading* (45-55°) *on the upper leaves,* in xeromorphic, small-leaved extremes also sometimes on the lower leaves, normally on mature stems with *lower leaves obliquely spreading* (65-75° usually), *but with postical margins almost invariably remaining at an acute angle* (65-80°, rarely 85°) *with* stem; leaves very *narrowly, obliquely ovate-lingulate,* on juvenile leaves and on weak stems sometimes more distinctly ovate, *widest clearly in the basal fourth, the postical margin weakly but distinctly ampliate above the base,* nearly straight above the dilation and *slightly and gradually converging to the nearly straight antical margin,* the leaves slightly and gradually, but *perceptibly narrowed from the basal fourth* to the rounded-truncate apex; leaves of mature shoots ranging from 775-850 (900-970) μ wide x 1600-1800 (2000) μ long, *averaging* (1.9) 2.0-2.25 (2.4) × *as long as broad,* on xeromorphic shoots sometimes only 740-850 x 1240-1360 μ long; *postical leaf-bases very short-decurrent,* the narrow decurrent strip and margin immediately above *narrowly erect, but not reflexed, the stem remaining prominently exposed;* dorsal base rather long-decurrent (weak forms) to prominently long-decurrent (strong forms), the antical margin narrowly but sharply reflexed for at least

half the length of the leaf; leaves normally *rather weakly serrate-dentate,* the dilated *postical base without teeth,* or rarely with a single obscure one, the postical margin above base usually with (3) 4-6 (7) low but sharp teeth, the narrowed apex usually with 2-4 teeth, of which 1-2 may be considerably larger, but hardly lobe-like, the distal one-fourth of antical margin commonly with (0) 1-2 weak teeth. Cells with walls ± thin, the trigones varying from moderate and concave-sided to rather large and bulging, not or exceptionally subconfluent, with intermediate thickenings absent except from leaf-middle, where rare, to base, where frequent; apical cells *ca.* 18-20 x 20-23 (25) μ; median cells (18) 21-24 x 24-32 (34) μ; cells at middle of postical margin 15-20 x 23-32 μ, their tangential inner walls not or hardly thickened; basal cells 22-24 x 29-38 μ or to 32-45 μ long; cells of teeth little elongated, the terminal acute triangular, *ca.* 21-24 μ long x 12-15 μ. *Oil-bodies very coarse-segmented* (more so than is normal for *P. floridana*), often only 2-4 or 3-5 segmented, the segments large and in a single row, occasionally with 6-9 segments, and then segments in part in two rows, 4-9 per cell, usually ovoid or ellipsoid to fusiform, 3 x 6-7.5 μ to 3-4 x 12.5 μ, rarely to 4.5 x 10 μ; chloroplasts 3-3.5 μ. *Underleaves superficially appearing nearly or quite absent,* obsolescent, in actuality reduced to 1-several minute cilia, of which one may be somewhat elaborated, ending in slime papillae, never with conspicuous lamellate lacinia. Asexual reproduction via *propagula,* produced from the distal portion of the postical faces of the leaves, and *often also on antical leaf face,* adjacent to postical margin.

Dioecious. Male plant unknown. Gynoecial plants with usually 2 subfloral innovations that may be again swiftly floriferous, and again bear innovations, leading to ± complex gynoecial systems. Bracts narrowly ovate-lingulate, similar in shape to leaves, (1450) 2150-2250 μ long x (780) 1000-1150 μ broad, often slightly falcate, *sharply but not coarsely spinose-dentate, the postical base often with rather crowded but smaller spinose teeth* (usually 4-6 per bract), but sometimes with only 1-2 teeth, the postical margin above base with 9-12 unequal, strong teeth; narrowed apex with 2-3 teeth usually; the antical margin revolute to or nearly to apex, with 2-5 small but sharp serrations. Perianth (unfertilized only seen) 1350 μ wide near the broadly rounded-truncate mouth x 1800 μ high, *irregularly but not very closely spinose-dentate, the teeth not crowded,* not laciniform, slender, ending in 4-6 superposed, single cells; dorsal and ventral keels subequal in length, the *antical obsoletely to distinctly winged for most or for its entire length,* the wing ending as a dilated auricle inserted on stem below, usually *with a few minute serrulations near apex.*

Type.—"Mexico apud Colipa" (*Liebmann*). The type material, in the Gottsche Herbarium at Berlin, has been destroyed. I have not seen duplicates of the type collection (or schizotypic plants); therefore, the diagnosis has been derived almost wholly from Floridian plants (*Schuster* 33324, Aspalaga Bluff, Gadsden Co.).

Distribution.—A neotropical species, restricted in the United States to a limited region of the outer Coastal Plain, extending from Louisiana to central and (somewhat questionably) southern Florida, northward represented by deviant but evidently conspecific material from South Carolina and North Carolina, where rare and local.

Apparently largely restricted to the West Indies and Central America, ranging from Mexico (*Liebmann, fide* Gottsche), to Puerto Rico (*Sintenis;* also a specimen seen from Laguna San José, Rio Piedros, *Pagan* 416), Cuba (*Wright*), southward to Valencia (Venezuela? *Fendler, fide* Stephani), and Bolivia (Tres Cruces, Cord. de Sta Cruz, 1400 m., *Herzog* 3556, *fide* Herzog and *fide Stephani!*). Typical, robust female plants have also been seen from Puerto Rico (Aibonito, *Pagan* 577!, mixed with *P. hypnoides*).

In the United States not previously reported. The following records of material that is presumably conspecific:

FLORIDA: "Buzzards Roost," W. of Gainesville, Alachua Co. (*Schuster* 33416, 33417, 33360); Aspalaga Bluff, on Apalachicola River, Gadsden Co. (*Schuster* 33324); "Devil's Millhopper," NW. of Gainesville, Alachua Co. (*Schuster* 33475, 33475a, 33476, 33480; *Anderson* 5271!); on *Hicoria,* Aucilla R. at Nuttall's Rise, Jefferson Co. (*Kurz* 128!; listed as *P. floridana* in Kurz & Little, 1933); Gainesville (*N. L. T. Nelson* 57, 57A; with perianths; listed as *P. floridana* in Kurz & Little, 1933); Highlands Hammock State Park, 6 mi. W. of Sebring, Highlands Co. (*Schuster* 19954b, *plate*!; 20106a, 26301, 26004, 26014, 26011a, *all var. integrifolia*); hammock forest at Juniper Springs, Ocala Ntl. Forest, Marion Co. (*Schuster* 31934); hammock forest near Hillsborough River, Hillsborough River State Park, Hillsborough Co. (*Schuster* 33937); Alum Bluff, Apalachicola River, Liberty Co. (*Schuster* 33537); deep hammock forest, Collier-Seminole State Park, Collier Co. (*Schuster* 26179a; var. *integrifolia*); Section 24, Long Key Pineland, Everglade Key, Everglades National Park, Dade Co. (*Schuster* 22050, 22097; var. *integrifolia*). LOUISIANA: Bois Lobbe (*Langlois* 622!; in herb. Yale as *P. smallii* Evs.; material sparse, but with both antical and postical propagula, with rather widely spreading leaves; trans. ad *P. floridana*?); near St. Martinsville (*Langlois* 622!; superficially trans. ad *P. floridana,* but leaves lingulate-ovate).

Less certainly to be referred here, but almost surely conspecific are plants from:

MISSISSIPPI: Over moist shaded, sandstone-limestone ledge, *ca.* 2 mi. E. of Route 49, near Saratoga, Simpson Co. (*Schuster* 19167a; questionable, see *P. floridana*). LOUISIANA: Base of gum tree, Sulphur Springs, near Covington, St. Tammany Parish (*F. Pennebaker,* B-3!). SOUTH CAROLINA: Swamp 8 mi. S. of Bamberg Co. (*Schuster* 33982, 33973; plate!). NORTH CAROLINA: Swamp 1.5 mi. E. of Whiteville, Columbus Co. (*Schuster, Blomquist and Bryan,* 30001b, plate!; *Schuster and Blomquist* 29228).

Some of the plants listed above represent deviant phases and are discussed below, separately. In addition, some of the material reported in the literature (Frye and Clark, 1944; Redfearn, 1952; Kurz and Little, 1933) as *P. floridana* belongs here; I have also seen material collected and named by Schornherst, labelled *P. ludoviciana,* that is apparently referable here, but the material is so sparse a certain determination is impossible. Much of the material seen in the

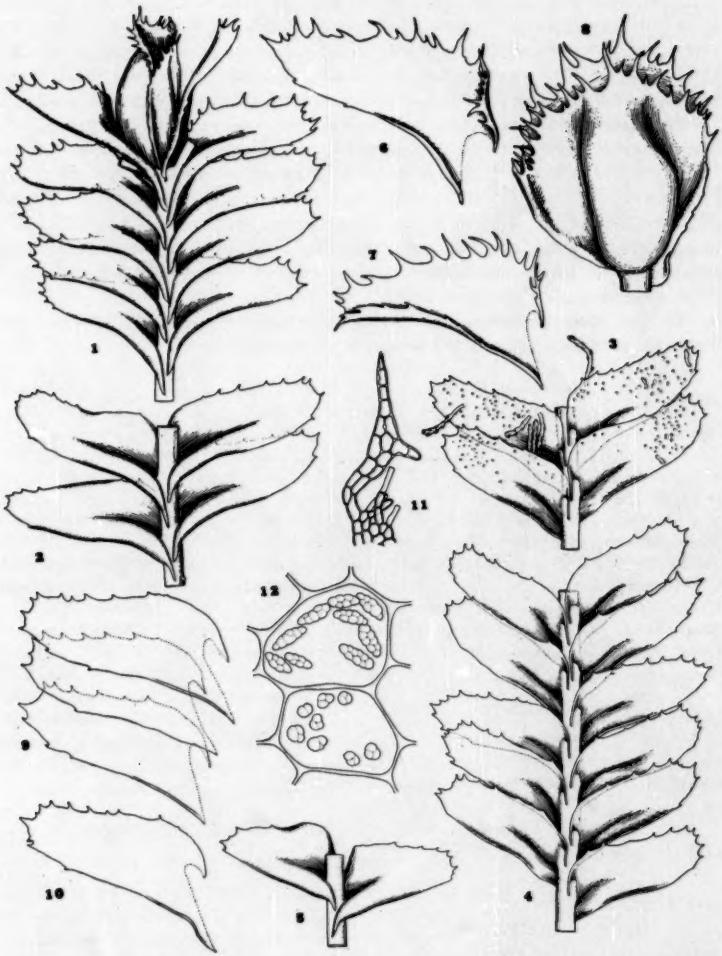

Fig. 50.—*Plagiochila dubia* Gottsche. 1. Perianth-bearing shoot, the innovations cut off near base (x 11.5); 2. Robust shoot-sector, antical aspect (x 15); 3. Postical aspect of propaguliferous shoot (x 11.5); 4. Typical shoot-sector, postical aspect (x 11.5); 5. Sector of large shoot, lower portion, showing leaves with maximal basal dilation (x 11.5); 6-7. Female bracts (x 15); 8. Juvenile perianth in lateral aspect, dorsal keel at right (x 20); 9-10. Leaves (x 15); 11. Large underleaf (x 93); 12. Median cells with oil-bodies (x *ca.* 560). (Figs. 1-5 drawn to same scale; figs. 6-7, 9-10 drawn from same scale; all from *Schuster* 33324, Aspalaga Bluff, Florida.)

P. dubia-floridana complex, indeed, appears so impoverished that a certain determination is impossible.

The identity of our plants with some of the Central American and South American plants referred to as *P. dubia* is very questionable. For example, the plants from Costa Rica (Bozuca, *A. Tonduz* 15658; in herb. Yale), determined by Stephani, have much more remote leaves, a firmer, reddish-brown stem, and a more robust size than the most luxuriant Floridian plants. By contrast, the Bolivian plants ("Bergwald von Samaipata," 1600-1700 m., *Th. Herzog* 6109!), also determined by Stephani, probably belong here. These plants, for example, show the diagnostic development of propagula of the *antical* faces of the leaves, as well as the more copious, "normal" production of propagula of the postical leaf faces. A third collection, also in the herb. Yale, from Bolivia (Cordillera v. Sta. Cruz, *Th. Herzog* 3499) is of totally unrelated plants; the plants are dense-leaved, belong to the Crispatae, and are clearly allied to *P. blepharobasis* Herz. (see Herzog, 1932, p. 216). They possess much more longly decurrent postical leaf-bases than does that species, although the sharp dentition is confined to these decurrent bases; the postical leaf-margins are crispate much as in *P. undata*. These plants appear to represent an undescribed species.

Ecology.—In our area apparently common on shaded, but relatively dry coral limestone ledges. Associated there with various other Hepaticae, chiefly the Lejeuneaceae, *Lejeunea minutiloba, L. calcicola, Crossotolejeunea bermudiana,* and also *Dumortiera nepalensis* and *hirsuta,* as well as various tropical ferns (*Asplenium heterochroum, verrucundum, Goniopteris reptans,* etc.). The plant, in such sites, is relatively well-developed, shows a reasonable amount of pseudodichotomous branching, occasionally bears perianths, and freely develops propagula. The plants are always distinctly dentate-leaved, and correspond rather closely to the concept of *P. dubia* that can be derived from Gottsche's (1863) figures and diagnosis.

In addition to such calcicolous, robust plants, one finds two other types of plants which are referable evidently to *P. dubia,* partly as impoverished forms. Firstly, and most surely, are corticolous plants from northern Florida to North and South Carolina, found in wooded swamps along slow-moving coastal streams. Here they occur on the bark of *Nyssa aquatica, Planera aquatica* and other trees, associated with *Plagiochila undata, Metzgeria cf. myriopoda, Radula caloosiensis* (*cf. langloisii*), *Rectolejeunea maxonii,* and (in several stations) *Plagiochila yokogurensis fragilifolia.* At the North Carolina station, furthermore, are associated the orchid *Epidendrum conopseum* at its northernmost locality, and *Lopholejeunea muelleriana* at its northernmost locality. The corticolous swamp plants are somewhat less robust (2.8-3.4 mm wide), have uniformly unbranched aerial shoots, or rarely a single dichotomous fork, and are wholly sterile, although propaguliferous. They agree with the saxicolous phases of *P. dubia* in dentition (that of the South Carolina plants is, if anything, coarser than normal; that of the North Carolina plants less coarse than usual, but distinct), leaf-shape and oblique orientation, and in the vestigial underleaves. It appears wholly impossible to consider these plants as other than a strongly reduced phase of *P. dubia,* with which they agree

in the facies when dry (leaves only slightly deflexed, stems not or slightly arched). Clearly allied to the swamp plants alluded to above is material from the "Beech-Magnolia" type of Mixed Coastal Forest, as for example, plants from bark of Beech, ravine in Alum Bluff, Apalachicola River, Liberty Co., Florida (*Schuster* 33537; p.p., with *Plagiochila ludoviciana, Cheilolejeunea rigidula, Ceratolejeunea laetefusca*).

Much less surely referable to *P. dubia* are even more reduced plants occurring in Florida, apparently exclusively in the southern third of the state. These have subentire to finely denticulate leaves that are often somewhat more imbricate, more dilated along the postical bases (which may be slightly shingled, frequently to the point where the stems, in postical aspect, almost "disappear" from view), and, in drying, have the simple aerial stems arcuate, almost terete in appearance, with the deflexed and tubularly convolute leaves erect and lying, in two lines, beneath the stem. The dry stems, as a consequence, are rigidly arcuate, and appear almost filiform! Associated with this, the plants in some cases tend to develop (with age) leaves that drop irregularly from the older portions of the axis. These plants, furthermore, tend to have the moist leaves suberect (Fig. 51:8), although occasionally more widely spreading (Fig. 51:9) on older axes. The few plants of this type seen have a weakly and remotely dentate perianth-mouth. Plants of this type appear restricted to the lower trunks of trees in evergreen hammock forests, where they occur on the bark of *Quercus virginiana, Citharexylem fruticosum,* and other trees. Associated are *Plagiochila ludoviciana, P. hypnoides, Ceratolejeunea laete-fusca, Cheilolejeunea* (*Euosmolejeunea*) *rigidula, Radula australis, Mastigolejeunea auriculata, Lopholejeunea subfusca,* and other *Lejeuneae,* and occasionally such ferns as *Polypodium plumula* and *Campyloneurum phyllitidis.* These plants, referred to a var. *integrifolia,* are discussed at length, below.

Differentiation.—*P. dubia* is distinguished by a most appropriate name. The species, in the existing literature, is not sharply separated from several species of the Sectio Hypnoides, and appears to be especially confused with *P. hypnoides* itself, as well as with its immediate relatives. The identification of the material from Florida with *P. dubia* rests upon comparison with plants from *Bolivia* (*Herzog* 3556!) and from Puerto Rico (*Pagan* 416!) and with the illustrations and descriptions of Gottsche (1863).

Three of the numbers cited above were also submitted to Dr. Th. Herzog, the eminent specialist on tropical Hepaticae. Dr. Herzog states: "Nach meiner Meinung könnten alle 3 als kleine Formen zu *P. dubia* L. et G. gerechnet werden. . . . Ihre Pflanzen sind etwas zwergig im Verhältniss zu der Abbildung bei Gottsche und, wie Sie sehen, auch zu den Exemplaren (Bolivia, *leg.* Herzog), die ich Ihnen beilege, und die von Stephani bestimmt wurden."

P. dubia is characterized essentially by the following ensemble of features: suberect to obliquely spreading leaves, rarely spreading as much as 75° from the stem, except on old shoot sectors; narrowly ovate-lingulate leaves, often with a very slight but characteristic sigmoid curvature (Figs. 49: 4; 50: 2); rather freely pseudodichotomous branching when mature; free propagulum production, with very often a few propagula produced from the distal portions of the antical face

—a most unusual feature; contiguous to slightly imbricate leaves, very short-decurrent postically, with the postical stem faces extensively exposed. The local material is often only questionably identifiable.

The Floridian plants differ, in part, in (a) less robust growth; (b)

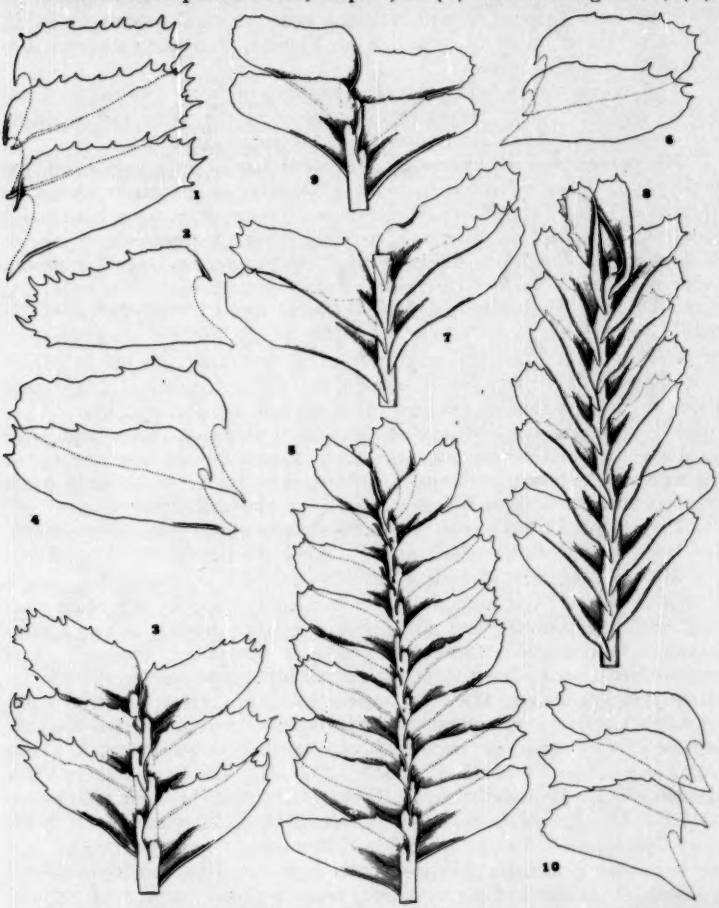

Fig. 51.—*Plagiochila dubia* Gottsche. 1-2, 4, 6, 10. Leaves (x 14.5); 3, 5. Shoot-sector, postical aspect (x 12.5); 7. Robust shoot-sector, antical aspect (x 12.5); 8. Shoot of extreme with erect-convolute leaves when dry, and subcircinate shoots (x 12.5); 9. Shoot of plant of type in Fig. 8, older portion, with patent leaves, postical aspect (x 12.5). (Figs. 1-2, 4, 6, 10, drawn to same scale; 3, 5, 7, 8-9 drawn to same scale; Figs. 1-3, *Schuster* 33973, Bamberg, South Carolina; 4-7, *Schuster* 30001b, Whiteville, North Carolina; 8-10, var. *integrifolia, Schuster* 19954b, Highland Hammock, Florida.)

nearly pure green color, with even the stem hardly brownish; (c) somewhat less strongly dentate leaves, with the teeth less sharp. These differences, as is seen under the discussion of *P. ludoviciana* (which undergoes very similar patterns of variation), are easily attributable to environmental causes. As with so many other tropical species, *P. dubia,* at the northern edges of its range, in Florida, is consistently less luxuriant than in the tropics.

The relationships with several members of both the Sectio Contiguae and the Sectio Hypnoides occurring in the West Indies, Mexico, and the Appalachian region are "uncomfortably" close.

My concepts of *P. hypnoides* are based partly on plants from the herb. Montagne, collected in Cuba (NYBG), on plants collected by Wright in Cuba (Hep. Cub. Wrightianae), on a series from South and Central America (leg. Herzog), as well as on the figures and discussion in Carl. *P. dubia* differs from *P. hypnoides* in several respects, principally in the lack of discrete underleaves and in the less imbricate as well as less dilated or ampliate postical bases of the leaves. The leaves, as a consequence, do not completely obscure the under surface of the stem on main stems, and the postical leaf-bases are not or slightly shingled. In *P. hypnoides* proper, the dilated postical leaf-bases, when *in situ,* extend across and often slightly beyond the stem. Correlated with this, the leaf in *P. hypnoides* is obliquely ovate-triangular in shape and tapers conspicuously from shortly above the base up to the narrowly subtruncate apex. Contrastingly, that of *P. dubia* is more nearly parallel-sided, and tapers slightly in the *distal half.*

These distinctions nearly or quite disappear in juvenile material. In *P. hypnoides, P. floridana* and *P. dubia* the upper leaves of shoots are always obliquely spreading or suberect (45-55, rarely 65° angle with stem apex); the juvenile leaves in all three species are often narrow, with the postical base not ampliate or only slightly so; as a consequence, the postical face of the stem is extensively exposed. The separation of such juvenile forms of the three species should not be attempted, since there does not appear to be any good basis for a definitive separation. Excellent examples of such juvenile forms are collections of *P. hypnoides* (presumably) from Brogdon Hammock, Dade Co., Florida (*Small and Mosier* 6232; Fig. 60), and from Palma Vista Hammock, Everglades National Park, Dade Co., Florida (*Schuster* 22148). The first of these was determined by A. W. Evans as *P. floridana* "probably." In the latter case, the upper, younger leaves are erect-spreading, and the shoot has a strongly "*P. floridana*-like" aspect.

Both *P. dubia* and *P. hypnoides* seem to have an almost equally extensive range in the coarseness of the teeth. In robust, coarsely dentate forms, the dentition may extend down along the postical margin to the dilated basal region. By contrast, more slender (usually shade) forms have lower, often subobtuse teeth, and the teeth are fewer and restricted to the distal one-third of the leaf. A valid distinction between the two species appears to lie in the degree of development of these teeth near the postical leaf-bases. In *P. hypnoides,* they always extend down to the decurrent postical bases of the leaves, and are

sharp and conspicuous there. In all forms of *P. dubia* seen they are obsolete or absent near the postical bases, becoming more distinctly developed in the distal two-thirds of the postical leaf-margins.

In the relatively narrow leaves, with the postical base only slightly dilated, *P. dubia* very closely approaches the southeastern *P. floridana* Evs. This similarity is enhanced by the fact that the upper halves of most shoots, in *P. dubia*, show oblique leaves (spreading at an angle of 45-55°). In fact, such shoots may show such a marked similarity that a separation of the two species sometimes appears almost impossible. This is particularly true of small, xeromorphic, phases. The similarity is enhanced by the close agreement in cell size and form of the oil-bodies. However, the mature, main stems of *P. dubia* show widely spreading leaves (65-75°), whose anterior (postical) margins generally lie nearly, if not quite at right angles to the stem. Juvenile or poorly developed plants of the two species appear virtually inseparable.

Part of the difficulty with respect to the identification of *P. dubia* is directly attributable to environmental causes. The xeromorphic, corticolous forms (such as a very small phase, only 1.8-2.2 mm wide, from the base of *Quercus virginiana*, in the drier portions of Highlands Hammock, *Schuster* 19954b) often have the leaves quite suberect, even on mature portions of shoots (Fig. 51:8), and are therefore extremely difficult to separate from the usually equally small *P. floridana*. However, even in such phases the leaves are more dilated postically (Fig. 51:9-10), particularly on the less mature, lower portions of shoots (Fig. 51:9). Such ovate-triangular leaves simply do not occur in normal *P. floridana*. Perhaps significant in the disposition of such xeromorphic forms is the difference in form of the oil-bodies, as contrasted to those of *P. floridana*. In *P. dubia* var. *integrifolia*, to which these small phases of *P. dubia* are here referred, usually 4-8, rarely 9, oil-bodies occur in the median cells, and these are very coarsely segmented, while in *P. floridana* there are 6-11, occasionally 12, oil-bodies per cell, and these are formed of smaller and more numerous segments (compare Fig. 53:6-8, with 53:1).

In addition to the disturbingly close relationship to *P. floridana* of the Coastal Plain, *P. dubia* exhibits unmistakable similarities to the Appalachian *P. virginica-caroliniana* complex. From this it differs in two principal ways: (a) the upper leaves are much more erect-spreading, at usually nearly a 45° angle with the stem; (b) mature shoots have the leaves, except the basal leaves of branches, non-falcate, clearly much more elongate, averaging 2.0-2.4 × as long as wide. In the *P. virginica-caroliniana* complex the upper and lower leaves, upon attaining their definitive size, are essentially similarly oriented and widely spreading; they also average much less than 2.0 × as long as wide under normal circumstances. In other respects (cell size; oil-bodies; dentition of the leaves; slightly decurrent and noncristate postical leaf-bases; vestigial underleaves) *P. dubia* may agree very closely with *P. virginica*. The very close affinity of *P. dubia* and *P. virginica* is particularly well brought out in corticolous plants, from Alum Bluff, Liberty Co., Florida (*Schuster* 33537). These plants have the sharply dentate leaves of *P. virginica*, with two of the terminal teeth often elaborated in a lobe-like fashion; they have the mature leaves widely

spreading (at an angle of 65-76°; with the postical margins at nearly right angles with the stem!); they have partly distinctly falcate leaves, with the dorsal base conspicuously long-decurrent. Yet the narrow leaf-form and the occasionally obliquely spreading leaves force one to consider them to be deviant *P. dubia.* The Alum Bluff plants occur with *P. ludoviciana.* It is noteworthy that, under the particular environmental conditions pertaining at this site, the *P. ludoviciana* is strongly chlorophyllose and deep green, the *P. dubia* is relatively pellucid and light green. In general, the latter "tends" to be a paler plant than the quite chlorophyllose, more opaque *P. ludoviciana* and *P. hypnoides.* Furthermore, the propagula, which occur in abundance, are found sparingly on the antical face of the distal halves of the leaves, as well as more abundantly on the postical (abaxial) faces, typical of *P. dubia;* in the wide range of plants of *P. virginica* seen, no antical propagula have been seen, although they possibly have been overlooked. It is possible that the Alum Bluff material (Fig. 49:8-16) represents an impoverished phase of the Mexican *Plagiochila acanthoda* Ldbg. et Gottsche, or of the Mexican plant called by Gottsche (1863) *P. chinantlana* var. *b.* Compare the figures here given for the Floridian plant with Gottsche (1863, pl. 5). Until more copious material becomes available, it appears best to retain the Floridian plant in *P. dubia,* although it forms a deviant element in that species. Note should also be taken of the fact that the Alum Bluff material shows close similarities in many respects to *P. intermedia* Ldbg. et Gottsche, *P. apicalis* Gottsche, and to a lesser extent to *P. expansa* Gottsche, species all described and illustrated by Gottsche. It appears certain that Gottsche was overly optimistic about the sharpness of some of the distinctions he utilized to separate these species, and that future study will demonstrate the need for synonymy in this complex. At such a time, the status of the present collection will need to be reinvestigated.

Variation.—As is evident from the preceding discussion, *P. dubia* appears to be a polymorphous plant, subject to wide latitudes in variation. It is possible the species is too broadly interpreted here, and that the plant which is subsequently segregated as var. *integrifolia* deserves separate specific rank. However, the limited number of collections from our area suggest that, for the time being, a conservative treatment is desirable.

The typical plant, as typified by the illustrations and description of Gottsche, and the plants from Aspalaga Bluff, Florida (*Schuster* 33324; see Fig. 50), is a robust plant, 3.5-4 mm broad. The plants most closely similar to those from Mexico, illustrated by Gottsche, are the Aspalaga Bluff plants (Fig. 50), which agree in size, in the shape, insertion, orientation and dentition of the leaves, in the shape and dentition of the female bracts (and in particular, in the irregularly spinose dentition, with the postical bases with several rather crowded teeth!), in the presence of a dorsal keel of the perianth, virtual lack of underleaves, and all other salient characters. Only the perianth mouth appears more irregularly and coarsely ciliate than in the Gottsche material. However, in the equally robust plants from the

"Devil's Millhopper," Gainesville, Florida (*Schuster* 33475a; Fig. 49: 1-7) and in plants from Gainesville, Florida (*N. L. T. Nelson* 57, 57A), the female bracts tend to be less sharply, and more regularly serrate-spinose, without the characteristic teeth of the postical leaf-bases, although the perianth mouth is more regularly, and less longly dentate with about 25-32 aciculate teeth per "lip" (and thus more closely approaches Gottsche's material); the perianth does not bear a dorsal keel, at least when juvenile. These two extremes, in the local plants, are bridged over completely by the equally robust material from the "Buzzard's Roost," W. of Gainesville, Fla. (*Schuster* 33416, etc.). In this material the bracts agree with those from the "Devil's Millhopper," i.e., are relatively moderately dentate, without spinose teeth near the postical base, as is the perianth mouth, which bears rather regular and rather numerous, relatively fine teeth. However, at least the antical base of the perianth is keeled, with the low keel elaborated at the juncture with the stem as a lamella. In this respect the plants closely approach those from Aspalaga Bluff. These three collections may be regarded as nearly typical of the species as any material from our region that has come to light. Until Mexican material becomes available, these plants may, indeed, be regarded as typical of the species.

Other aspects dealing with the variation in *P. dubia* have been previously dealt with above. The disposition of the troublesome small-leaved phases from the southern one-third of Florida, however, remains to be dealt with. These plants are perhaps best separated, at least tentatively, as follows:

P. dubia var. integrifolia var. n.
Figs. 51:8-10; 52; 53:6-8

Plantae multo minores quam *P. dubia;* virgae steriles 2.0-2.5 mm latae; caules plerumque simplices, sicci valde arcuati; folia sicca erecta, tubuloconvoluta, 1.55-1.75: 1; folii apex paene integer vel 2-3 dentibus parvis, inconspicuis praeditus; perianthii os paucis dentibus parvis, remotis, 2-3, raro 4-6 cellulas in longitudine praeditum. Typus: Highlands Hammock State Park, near Sebring, Florida (*Schuster* 26004 = *Schuster* 19954b); in herb. author.

Plants olive to brownish, rarely green, *much smaller,* 2.0-2.5 (on female shoots 2.8-3.0) mm wide. Leafy sterile aerial *stems simple,* usually scattered in occurrence (and not forming thick mats), *only* 8-16 *mm high,* arcuately spreading from substrate (vertical tree trunks), *strongly arcuate when dry,* (190) 200-235 μ in diameter. Leaves when *dry* $\pm$ *tubularly convolute, deflexed, lying erect in two juxtaposed lines beneath the stem,* when moist, erect-spreading (45-50°), to obliquely spreading (55-75°), *quite distinctly imbricate* (*in postical aspect, stem often nearly or quite hidden*), *narrowly ovate-triangular,* 1240-1360 μ *long* x 740-850 μ broad up to 1350-1625 μ long x 870-920 μ broad, only (1.45) *1.55-1.75* $\times$ *as long as wide;* apex rounded to rounded-truncate, *virtually edentate* or with 2-3 small to moderate, rarely coarse, teeth; *postical margin virtually edentate, or with 2-4 small and usually inconspicuous teeth.* Apical cells *ca.* 17-20 x 23-27 μ; median *ca.* 18-22 x 28-

35 μ; basal cells *ca.* 20-24 (26) x 29-38 μ; *trigones large,* but hardly confluent; intermediate thickenings occasional to frequent in cells of lower half of leaf; oil-bodies commonly only 2-4 to 5-6-segmented, the segments largely in a single row. *Propagula absent or usually only spar-*

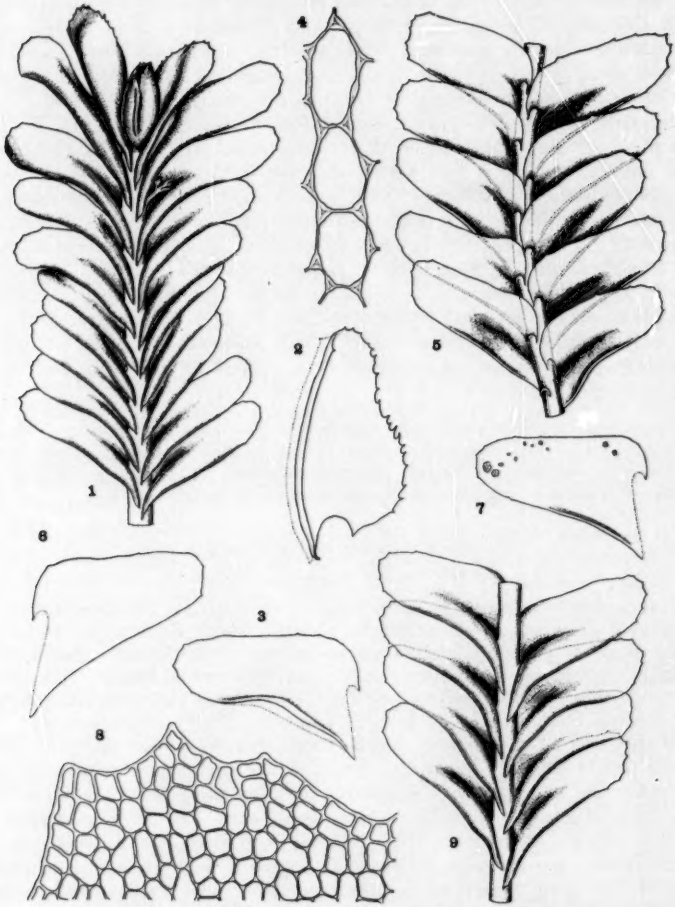

Fig. 52.—*Plagiochila dubia* var. *integrifolia* Schuster. 1. Plant with juvenile perianth (x 13.5); 2. Female bract (x 13.5); 3. Large leaf (x 13.5); 4. Median cells of base of leaf (x 410); 5. Part of shoot, postical aspect (x 19); 6-7. Leaves (x 16); 8. Apical cells of extremely dentate leaf-apex (x 160); 9. Shoot, dorsal view (x 16). (Figs. 1-3 from *Schuster* 22097, Long Pine Key, Florida; 4-9, *Schuster* 26004, Highland Hammock, Florida; for other figures of *Schuster* 26004 see Fig. 53:6-7.)

ingly developed, only on lower faces of leaves; *lower leaves sometimes tardily and irregularly breaking free,* but hardly caducous in the usual sense of that term.

Female bracts (from *Schuster* 22050, 22097) *ca.* 1950 μ long x 1175 μ broad, ovate-triangular, the postical margin above the *entire base with* 10-12 *or to* 15-16 *small, fine, relatively regular teeth* extending to and around the rounded apex. Perianth (juvenile; from *Schuster* 22050, 22097) with *few, small, distant teeth usually only 2-3, occasionally 4-6 cells long.*

Type.—Highlands Hammock State Park, near Sebring, Florida (*Schuster* 26004, 19954b), from bark of *Carya* and *Quercus virginiana,* p.p. (with *Plagiochila ludoviciana, Ceratolejeunea laete-fusca, Cheilolejeunea rigidula, Radula australis, Mastigolejeunea auriculata, Cololejeunea contractiloba,* etc., and the fern, *Campyloneurum phyllitidis*); *No.* 26004 may be considered the type (from this have been prepared Figs. 52:4-9 and 53:6-7).

Distribution.—Known only from a few collections from the southern third of Florida. Except for the type material, which is relatively copious, usually in small quantity and poorly developed, the collections from Collier-Seminole State Park, Collier Co. (*Schuster* 26179a; bark of *Xanthoxylum fagara,* with *Radula australis*), from Highlands Hammock, Highlands Co. (*Schuster* 19954b, 20106a, 26301, 26004, 26011a) and from the Long Key Pineland, Dade Co. (*Schuster* 22050, 22097) appear all referable to this extreme. The ecology of these plants has already been discussed; it is possible only an extreme environmental phase is at hand. However, the weakly dentate female bracts and perianth-mouth strongly suggest otherwise.

Discussion.—This plant is a small extreme, which may easily be confused by the beginner with juvenile phases of *P. hypnoides,* since it usually has the leaves so distinctly imbricate that the postical bases are shingled, thus hiding the stem from view (Fig. 51:9). The plant then belies its affinity with the Contiguae, and appears wholly different from "normal" *P. dubia.*

However, associated with such extremely dense-leaved plants one frequently finds individuals with somewhat less dense leaves, leaving the stem exposed to some extent, in postical aspect (Fig. 52:5). In either case, the plants differ from all phases of *P. hypnoides* in the vestigial underleaves and very weak or obsolete dentition, as well as in the non-cristate nature of the postical leaf-bases. It is possible that the plant deserves a higher taxonomic status than here accorded it. Although at first glance giving the impression of being a small, xeromorphic extreme of more "normal" *P. dubia,* such an interpretation seems an oversimplification. Although the Highlands Hammock material is partly from rather open hammock forests, on bark of trees such as *Carya* and *Quercus virginiana,* which frequent the less wet portions of hammock forests, the plants from Collier-Seminole and from the Long Key Pineland are from a very deep, evergreen type of hammock forest, of Caribbean affinity, as luxuriant and dense as can be found in Florida. Yet these plants are equally dense-leaved as the

Highlands Hammock material! The most robust material, to 2.8-3.0 mm wide on female plants, is that of *Schuster* 22050 (Long Key Pineland); it is also from the most shaded, humid site at which the variety has been found, yet is the densest-leaved of all the collections seen!

The collections from the stations referred here differ in minor respects from each other. For example, the material from Highlands Hammock (type; and *Schuster* 19954b, etc.) represents a strongly xeromorphic extreme, with a certain amount of brownish pigmentation, rarely exceeding 2.0 mm wide. The narrow leaves, somewhat dilated at the postical base, and the acute angle (40-45°) at which even the mature leaves spread, and the moderate size (*ca.* 2 mm wide) at once separate the plants from the accompanying *P. ludoviciana,* and place it near *P. floridana.* The plants bear a few propagula (while the accompanying *P. ludoviciana* is luxuriantly propaguliferous). In all foregoing features the plant approaches *P. floridana,* of the form with little spreading, suberect leaves. However, the older leaves of the plant show a marked tendency to be brittle and break off, even though there is no sharply marked caducous development such as we find in the *P. austini-sullivantii* complex (where even the young leaves may be caducous!). In the fragmenting of the leaves, the plants somewhat resemble *P. yokogurensis* subsp. *fragilifolia,* from which they differ at once in that only an irregular short stub (rather than the basal one-third to one-half) is left of the leaf, after fragmentation, in the suberect leaves, and in their scarcely dilated postical bases (as well as in the rare branching of aerial shoots, and in the much inferior size). Whether this tendency to lose the older leaves is widespread in the fo. *integrifolia* is impossible to tell at present. It has not been noted in more typical *P. dubia.* Loss of the older leaves is developed to a high degree in the scrappy plants from Juniper Springs, Florida (*Schuster* 31934, p.p. with *Radula caloosiensis* and *Cololejeunea contractiloba*). These plants are as small as in var. *integrifolia,* but bear the strong teeth of normal *P. dubia.* The plants are wholly deviant, and appear impossible to refer safely to any species except *P. dubia.*

The material from the third locality referred to above, from the Long Key Pineland (*Schuster* 22097, 22050) is from a much more mesic site, from dead lianas and roots in deep hammock forest; it shows even more reduced dentition, wholly lacks propagula, and has a slightly different facies. The larger plants (to 2.8-3.0 mm wide) are strongly dense-leaved, with the facies of a small, virtually edentate *P. hypnoides,* which they also resemble in that the leaves, when dry, are little convolute, and spread to some extent (rather than being erect and appressed to the stem, as in the type material). These plants, particularly those of *Schuster* 22050, give perhaps the best idea of the mature state of this variant. They also suggest strongly that the var. *integrifolia* is possibly a wholly distinct species, since (a) the admittedly juvenile perianths bear much shorter teeth at the apex, many of which terminate in slime papillae; the teeth are mostly 2-4 cells long, only a few attaining a length of 5-6 cells; (b) the perianths lack an antical wing; (c) the female bracts are weakly serrate-dentate, rather than irregularly spinose-dentate. The position of the gynoecia is identical with that typical of *P. dubia* s. str.: the leading axes either have gynoecia at the apex, which may develop two subfloral innovations, which are almost immediately again fertile; or, the leading axis forks pseudodichotomously, and each of the forks is almost immediately fertile, bearing usually each a single subfloral innovation, which may soon again be fertile. In either case, there is a tendency for clustered, sympodial gynoecia, with all but the original one that terminated a main axis situated on very short branches.

Although these plants are closely similar to juvenile *P. hypnoides*, they are clearly distinct in the generally less widely spreading leaves (postical margins only occasionally approaching a right angle with the stem), the vestigial underleaves, and the edentate basal portions of the leaves. The plants also exhibit some similarity to *P. floridana*, particularly in: the leaves on robust female shoots being largely at an angle of 45-55° with the stem (but on less robust sterile shoots often spreading more widely). The plants are of about the same size, sterile shoots attaining a width of 2.5-2.6 mm, female shoots of 2.8-3.0 mm. The underleaves are also equally minute to vestigial. The postical leaf-margin is equally short-decurrent. The resemblance to *P. floridana* ceases at this point, and the plant differs as follows: (1) Lateral leaves typically almost edentate, with at most 2-4 vestigial low teeth 1, rarely 2 cells high (coarsely dentate in typical *floridana*, at least near the leaf-apex). (2) Leaves narrowly ovate-rectangular and somewhat narrowed from base to apex, the subbasal width to *ca.* 920 μ, the length to *ca.* 1625 μ; *e.g.*, length distinctly less than twice the width (in typical *floridana*, leaf-length *ca.* 2-2.4 × the width, the leaf-shape nearly rectangular, little or scarcely dilated at postical base). (3) Female bracts narrowly ovate, rather distinctly dilated on basal half of postical margin, quite finely dentate with teeth rarely over three cells long (in typical *floridana* with postical margin little arching, the shape essentially subrectangular, the apex and postical margin with few coarse, spinose teeth). (4) Perianth-mouth with few, small teeth only 1-3 cells long (closely spinose-ciliate at mouth in typical *floridana*). (5) Juvenile leaves scarcely longer than wide to 1.4 × as long as wide, varying from short-ovate to slightly obovate, entire (bilobed or spinose-dentate and at least 1.5 × as long as wide in typical *floridana*).

PLAGIOCHILA FLORIDANA Evans

Figs. 53:1-5; 54-55A

Plagiochila floridana Evans, Bot. Gaz. 21:190, 1896.

Plants in green to brownish-green patches, with a sharp division into radicellose reduced-leaved, rhizomatous creeping stems and leafy aerial stems that stand away from their substrate. Leafy shoots usually 2.4-2.8, occasionally 3.0-3.2 mm wide x 10-15 (25) mm long. Stems firm, yellowish-brown, rather slender, *ca.* 180-225, occasionally 250 μ thick; branches few, diffuse, monopodial on weak shoots, but on robust shoots the *Frullania*-type branches nearly as vigorous as the stems, then *becoming pseudodichotomous;* gynoecia almost always with 2 subfloral innovations, appearing situated in the fork of a dichotomy. Leaves slightly to distinctly imbricated, horizontally *erect-spreading* (*at an angle of* 40-50° *on the upper portions of shoots, and usually even on mature shoots;* with age often more widely spreading, to an angle of 55-65°), *narrowly oblong to ovate-rectangular and not or hardly falcate* when mature, *sometimes almost rectangular* or weakly rectangular-falcate, from *ca.* 400 μ wide x 1100 μ long (type) to 520-530 μ wide x 1150-1200 μ long, occasionally 570-700 (800) μ wide x 1350-1550 (1620) μ long, rarely broader and only 575 μ x 1150 μ long (*length usually* 2.0-2.4, occasionally 2.2-2.5 × the width); leaf-insertion rather narrow, usually 0.85-0.9 the maximal leaf-width (*ca.* 480 μ when leaf is 520-530 μ wide), the *postical leaf-base short-decurrent, the antical leaf-base only moderately decurrent; antical margin nearly*

straight to slightly concavely arched, strongly reflexed for 0.6-0.9 its length, the cnemis a distinct narrow dorsal fold; median part of leaf depressed and broadly and shallowly sulcate-depressed for *ca.* 1/3 its length; *postical margin scarcely to slightly dilated above the base* and

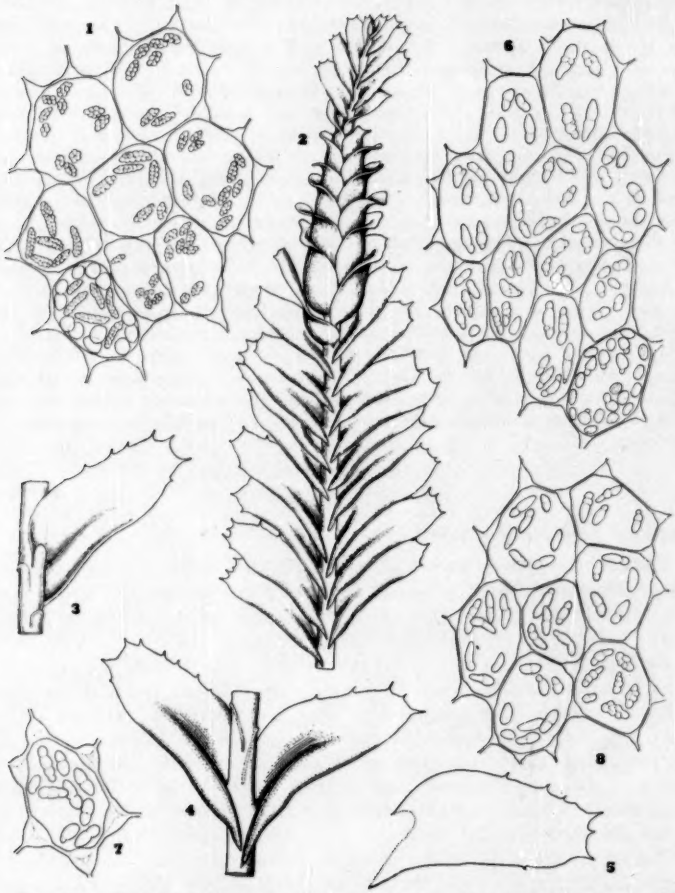

Fig. 53.—*Plagiochila floridana* Evs. 1. Median cells with oil-bodies (x 500); 2. Male plant, antical aspect (x 13); 3. Leaf, *in situ*, postical view (x 17); 4. Shoot-sector, antical aspect (x 17); 5. Leaf (x 17). *Plagiochila dubia* var. *integrifolia* Schuster. 6. Cells of leaf-middle, the lowermost with chloroplasts as well as oil-bodies drawn in (x 485); 7. Cell of mod. *pachyderma*, with oil-bodies (x 540); 8. Cells with oil-bodies (x 460). (Figs. 1-5, from *Schuster* 26013a; 6-7, *Schuster* 26004; 8, *Schuster* 26011a; all from plants from Highlands Hammock, Florida.)

arched, but distal two-thirds of margin virtually straight and *subparallel or only slightly converging to the antical margin,* the leaf thus often appearing nearly rectangular; *leaf-apex usually subtruncate, often appearing sharply but shallowly bilobed,* at other times 3-4 dentate; postical margin with occasionally 1-2, but more often usually 3-5 small, spinose, irregular teeth (the leaf-margin as a whole with 6-10 teeth, only juvenile leaves merely bilobed or bidentate; *apical two lobe-like teeth often characteristically divaricate*). Cells thin to moderately thick-walled, with small and concave to rather large, subconfluent trigones, the walls generally lacking intermediate thickenings; marginal cells in 1, rarely 2 rows somewhat to distinctly thick-walled and often forming a slight border (the tangential walls often rather distinctly irregularly, undulately thickened); cells at base of apical teeth usually 25-27 μ long along margin; cells along middle of postical margin variable, *ca.* 22-25 to 36-43 μ long x (13) 15-17 μ wide, often quite elongate and narrow, often thick-walled; marginal cells of postical base somewhat more elongate, usually distinctly thick-walled; cells of leaf-tip *ca.* 18-21 x (20) 22-29 μ, of leaf-middle *ca.* (17) 18-24 x 24-36 μ; basal cells of midline of leaf 22-25 (27) x 32-45 μ, not forming a vitta; trigones distinct, but usually quite concave-sided, in robust phases often large and bulging, the longitudinal intervening walls thickened, the cells thus appearing seriately thickened in longitudinal lines; oil-bodies 6-11 (12) per median cell, 3 x 5-8 (9) μ, a few to 3-3.5 x 10 μ, distinctly segmented of globules *ca.* 0.8-1.5 μ, usually arranged in 2 (-3) rows; chloroplasts 4.5-5 μ. *Underleaves minute,* usually lanceolate or of 2-several uniseriate cilia to lanceolate-ciliate, the segments commonly terminating in clavate slime-papillae. Asexual reproduction commonly present, by means of *leafy propagula of the postical (often also of the antical) leaf-surface.*

Dioecious. Male plants to 2.4 mm wide; androecia somewhat whitish-green, contrasted to the darker remainder of the plant, formed of 6-11 pairs of closely imbricate, ventricose bracts, which are erect (except for the distal 0.15-0.25, which is erect-spreading or spreading, or occasionally even reflexed); concave basal portions of bracts quite entire both dorsally and ventrally, the free, spreading portions varying from truncate to rounded and subentire to obscurely emarginate, or bidentate, with ill-defined teeth; bracts to 1200 μ long in basal portion of androecium, becoming progressively smaller distally, the compactly spicate androecium thus distinctly tapering, proliferating vegetatively distally. Female inflorescence at apex of main leafy shoots, usually eventually subtended by 2 (less often 1) innovations. Female bracts like leaves, but postical base more dilated, ovate-rectangular to subrectangular, 1000-1025 μ wide above base x 1750-1950 μ long, the entire *postical margin to the base coarsely spinose-dentate with ca.* 8-11 *teeth, the apex with* 3-5 *coarse spinose teeth.* Perianth (immature) broadly campanulate in lateral outline, wider than long, *not or obscurely winged, the two keels subequal; mouth longly, closely coarsely ciliate.* Mature (but sterile) perianth with bracts sheathing at base,

suberect to widely spreading, the perianth quite obvious, in dorsal profile ovoid, widest in basal third, to 1000 μ wide below x 1800-2000 μ long (in lateral profile widest near apex, the antical and postical "keels" subequal, *ca.* 1200 μ wide near the rounded-truncate apex); postical

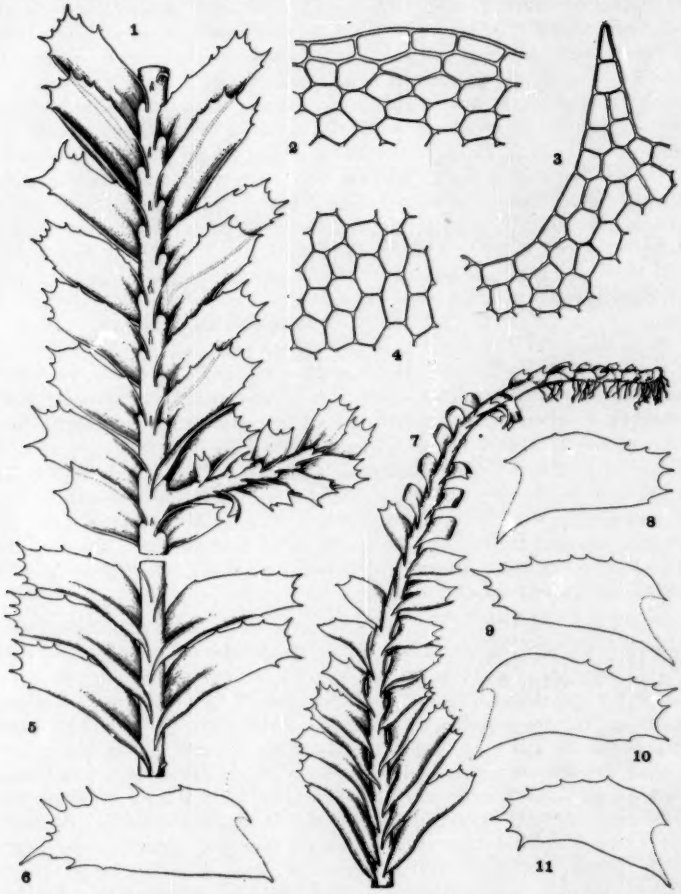

Fig. 54. *Plagiochila floridana* Evs. 1. Shoot-sector, postical aspect (x *ca.* 16); 2. Cells of middle of postical margin (x 205); 3. Cells of leaf-apex (x 205); 4. Median cells (x 205); 5. Part of robust shoot, antical aspect (x 14); 6. Leaf (x 19); 7. Apex of shoot with decumbent, rhizoidous apex (x 14); 8-11. Leaves (8-9, x 19; 10, x 21; 11, x 18). (Fig. 1, from type specimen; 2-5, 7-11, from specimen collected by Rapp, issued in Verdoorn's Hep. Select. et Crit. No. 386; 6, from plants collected at Alexander Springs, Florida, illustrated in Fig. 55.)

keel not carinate, antical keel weakly carinate in basal one-third to one-fourth, the keel edentate, but sometimes proliferated as a lobe-like wing at base of perianth or at juncture with axis; *mouth ciliate with spinose teeth 2-3 cells wide at base, terminated in up to 5-7 superimposed cells;* terminal cells spinose, tapering, *ca.* 15-19 x 32-46 μ, the uniseriate cell-row below formed of cells *ca.* 18-25 μ long x 20-22 μ broad.

Type.—Ocala, Florida (*L. M. Underwood;* Underwood and Cook, Hep. Amer. No. 109, sub *P. ludoviciana!*).

Variation.—*P. floridana* is apparently one of the less variable species among our *Plagiochila* flora. The above description is based on the type material, on a specimen collected at Sanford, Fla., by Rapp (distributed *in* Verdoorn, Hep. Select. et Crit. No. 386), on male plants (*Schuster* 26013a) from Highlands Hammock and on perianth-bearing plants from Alexander Springs (*Schuster* 31519). However, the variation in a) leaf-shape, b) leaf-orientation, c) dentition of the leaves, d) form and dentition of the female bracts, appears to be so considerable that some discussion appears necessary. To some degree, at least, the variation is probably the result of genetic differences.

Leaf-shape.—This is typically so rectangular that it closely simulates that of *P. diffusa.* However, the more coarsely dentate leaf, often bilobed at the apex, and the suberect leaves, as well as essentially immarginate leaves separate such material from *P. diffusa.*

In material such as the Rapp specimen (Verdoorn's No. 386), the leaves are slightly more dilated basally, and distinctly narrowly ovate-rectangular to ovate-falcate (Fig. 55A:5-7), but are dentate much as in the type (even though the terminal two coarse teeth are only exceptionally divergent). The Rapp material, on the basis of the sometimes less erect leaves, and the somewhat dilated postical bases, is perhaps related to *P. dubia.*

In closely allied plants referred to *P. dubia* the leaves become more ovate-falcate to ovate-rectangular, with a rounded apex and virtually entire margins (Figs. 49:4-5; 50:1-4, 9-10). Such plants are perhaps not specifically distinct, but depart so widely from the typical concept of *P. floridana* that it appears impossible to retain them in *P. floridana.* Unfortunately, a certain amount of transition in shape and dentition occurs.

Leaf-orientation.—Typically, *P. floridana* has the leaves of both the terminal portions of shoots, as well as older, mature leaves, spreading on each side at an acute angle (commonly 40-45°) from the stem-apex; this is well-illustrated in Fig. 54:1, from the type specimen, and in both the male and female plants illustrated (Figs. 53:2-4; 55:1, 5, 8).

However, much material shows only the upper leaves with the angle retaining the acute form (as in the Rapp specimen Fig. 54:5, 7), while the mature lower portions of shoots show the leaves widely spreading laterally (at an angle as high as 60-65°, as in Fig. 54:5, also drawn from the Rapp material).

In the subentire-leaved plants referred to *P. dubia* the angle again varies from *ca.* 48-50° to as high as 65°. Since the various keys (Evans, 1896; Frye and Clark, 1944) emphasize this as *the* differential feature of the species, it is evident that the determination of this species has been a source of considerable difficulty.

Dentition.—Typically the leaves are coarsely dentate with relatively irregu-

lar teeth (Figs. 54:1; 55:9-10); this is equally true of the Rapp material (Fig. 54:6-11), and of the male and female plants referred to the species (Figs. 53:3-5; 55:9-10). In several specimens, referred to the allied *P. dubia* (Fig. 51:8-10), the denticulation is obsolete or rather reduced, giving the plants a strongly deviant appearance. The Mississippi plants (Fig. 55A:1-4) are clearly transitional.

Denticulation of bracts.—Typically the bracts are ovate-rectangular with (6) 8-11 coarse to fine, spinose, strongly irregular teeth on the postical margin which point in varying directions (Fig. 55:6-7). In the allied *P. dubia* the often more strongly ovate bracts may bear smaller, more regular marginal teeth always more numerous (10-16 or more on the postical margin), and the denticulate apex is sometimes rounded (Fig. 52:1-2). As is evident from Fig. 50:6-7 *P. dubia* may have almost as coarse, although more numerous, teeth.

Unfortunately, there appears to be considerable diversity in the number and degree to which the teeth of the bracts are developed. In the type material, figured by Evans, the bracts are relatively short and rectangulate in shape; they bear a number of very coarse, spinose teeth on the distal halves and at the apex (usually 6-7 per bract), and several smaller teeth near the postical base. In the otherwise typical plants from Alexander Springs (Fig. 55:6-7) the bracts are more elongate, bear more numerous, less polymorphous, and generally less coarse teeth. The range of variation in this respect, however, is not great enough in available material to afford a total transition to the condition typical of *P. dubia*.

Development of collenchyma.—Typically, *P. floridana* has slight to hardly thickened cell-walls, except in the 1-2 rows of marginal cells, where the tangential walls are often rather considerably thickened, and has small to moderate trigones that do not bulge into the cell-lumen. However, much of the material shows coarse trigones, often somewhat ill-defined, that distinctly bulge into the cell-lumen. Associated, in extreme cases, the longitudinal cell-walls may be very considerably thickened, and rare intermediate thickenings develop.

The preceding outline suggests that the pattern of variability in *P. floridana* centers largely around a "normal" and "typical" extreme, with uniformly suberect leaves; coarse dentition; narrowly rectangulate, parallel-sided leaves whose postical bases are not or hardly dilated; female bracts with a limited number of coarse teeth, and an ovate-rectangulate to oblong shape; perianths with a closely spinose-ciliate mouth. The pattern of variation extends from this type to one with the older leaves more widely divergent, with a finer dentition and more or less rounded leaf apices; with narrowly ovate-rectangular leaves, whose postical bases are perceptibly dilated; female bracts with weaker dentition and a distinctly narrowly ovate shape; perianth with short, small and usually distant teeth. Plants with the latter series of characters fully expressed appear identical to the small phases of *P. dubia*, to which they are tentatively referred.

Male Plant.—The male sex of this species has been hitherto unknown. Since the female sex is known, this then becomes one of three regional species, known from both sexes.

The male plants (*Schuster* 26013a, Highlands Hammock, Fla.) are *ca.* 2.4 mm wide, thus subequal in robustness to the female plants. The androecia are more whitish-green in appearance than the rest of the plant, and are formed of 6-11 pairs of closely imbricate bracts, which

are ventricose and erect, except for the distal one-fourth to one-sixth (which is erect-spreading to spreading or occasionally even reflexed), the concave basal portion of the bracts are quite entire-margined, both dorsally and ventrally, while the free, spreading portion of the bract varies (in the single collection available) from rounded to subtruncate

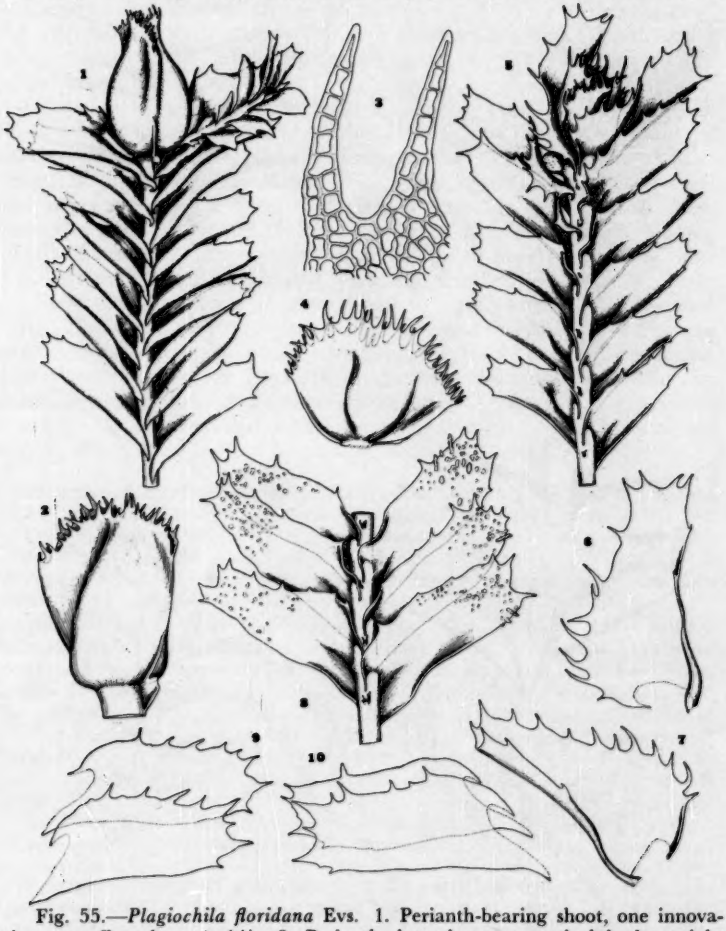

Fig. 55.—*Plagiochila floridana* Evs. 1. Perianth-bearing shoot, one innovation cut off at base (x 14); 2. Perianth, lateral aspect, antical keel at right (x 17); 3. Teeth of perianth-mouth (x 150); 4. Juvenile perianth (x 17); 5. Shoot apex with juvenile perianth, postical aspect, with one immature innovation (x 14); 6, 7. Bracts (x 17); 8. Sterile, propaguliferous shoot-sector, postical aspect (x 17); 9-10. Leaves (x 17). (All drawn from plants from Alexander Springs, Florida, *Schuster*.)

and subentire to obscurely emarginate or retuse (with rounded or obtuse, shallow lobes), to very obscurely bidentate, with ill-marked teeth. The male bracts are up to 1200 μ long, in the basal portion of the androecium, but become progressively smaller distally. As a consequence, the compactly spicate androecium tapers distally. Although terminal

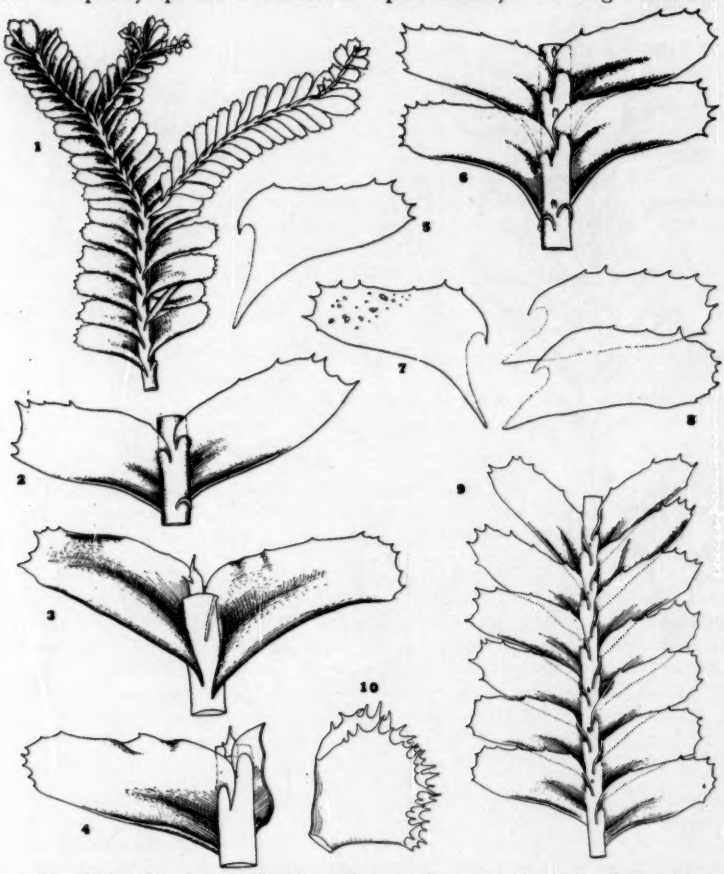

Fig. 55A.—*Plagiochila floridana* Evs. grading into *P. dubia* Gottsche. 1. Shoot-sector, with furcate branching and two gynoecia (x 6); 2-3. Shoot-sectors, in postical and antical aspect, in 3 with unusually large, atypical underleaf (x 18); 4. Leaf and large underleaf, *in situ* (x 18); 5. Leaf (x 10); 6. Shoot-sector, postical aspect (x 10); 7. Leaf with propagula (x 10); 8. Two leaves (x 16); 9. Shoot-sector, postical aspect (x 11.5); 10. Juvenile perianth, lateral view (x 18). (Figs. 1-4 from Mt. Olive, Miss., *Schuster;* 5-7, from Sanford, Fla., *Rapp,* Dec. 1903 (NYBG); 8-10, from *Webster and Wilbur* 756, Mississippi.)

at first, the apex of the androecium proliferates in all examined cases, forming a new vegetative shoot, whose basal 3-4 pairs of leaves are smaller than normal, merely 1-3-dentate at the apex.

In the virtually entire-margined male bracts, *P. floridana* exhibits a similarity to many other species of the genus, in which the male bracts are less dentate than the vegetative leaves. In the present case, the vegetative leaves are distinctly dentate with sharp, if not excessively salient teeth. The androecial region, as a whole, varies from 2.4-4.0 mm in length.

Distribution.—Evidently a local and rather rare species, found in Florida largely in the central, "Oligocene Island" region, and to the north, and extending westward along the Gulf Coastal Plain to Mississippi and probably Louisiana. The range of the species northward and westward from Florida is uncertain since in the Coastal Plain from Georgia to North Carolina, and from Mississippi to Louisiana, all the material in this complex appears rather poorly developed and is either transitional to *P. dubia,* or better referred to the latter.

The species appears to be confined to "old" areas in the Coastal Plain; in Florida chiefly found in the "Oligocene Island" area, where so many "old tropical" species occur; on the Gulf Coastal Plain found in the relict station for *Trichomanis petersii* (Mississippi) and in the rich "Beech-Magnolia" Forests, on *Magnolia grandiflora,* associated with *Halesia diptera, Illicium floridanum, Ilex opaca,* etc. (Mississippi; see Schuster, 1954).

FLORIDA: Alexander Springs, Ocala National Forest, Lake Co., c. perianth (*Schuster* 31519); Monroe, Seminole Co. (*Rapp, Jan. 1934;* issued as No. 386 in Verdoorn's Hep. Select. et Crit., and erroneously labeled as from "regione originali"); "Balanced Rock," edge of Chipola R. flood-plain, 7 mi. NE. of Mariana (*Kurz* 148! mixed with *Cololejeunea ornata;* plants less dentate than typical *P. floridana,* but with subtruncate leaf-apices); near Oviedo (*Rapp* 85! with antical as well as postical propagula; with *P. hypnoides*); below Juniper Springs, along Juniper Creek, Ocala National Forest, Marion Co. (*Schuster* 33460, *c. per., c. propagula; Schuster* 33454, *c. propagula*); Hardaway Tract, Liberty Co. (*Schornherst* 314!); Hillsborough River State Park, Hillsborough Co. (*Schuster* 22853a, 33905a, male). Highlands Hammock State Park, W. of Sebring, Highlands Co. (*Schuster* 26013a, male). [Also reported from Collier, Dade, Polk and Seminole Cos. (*fide* Redfearn, 1952) and Apalachicola R. bluffs (*Schornherst,* 1939); Mariana, Jackson Co. (*McFarlin,* 1934); Sanford (*Rapp,* Dec. 1903!; *No.* 30!; Rapp, 1934); Suwannee R. in Suwannee Co. (*Schornherst,* 1939); *fide* Frye and Clark (1944). These reports wholly unreliable, except for the Rapp material.] MISSISSIPPI: *Trichomanis petersii* locality, near Mt. Olive (*Schuster,* Aug. 1951; plate); De Soto National Forest, W. of Hwy. 49, *ca.* 14 mi. N. of Gulfport, along Big Biloxi R. (*Webster and Wilbur* 756 p.p., with *Rectolejeunea maxonii*). CUBA: Sierra de las Yuguas, San Diego de los Banos, Pinar del Rio (*Br. Leon* 5241; questionable material, with androecia, referred to *P. ludoviciana* by Evans; NYBG).

In addition to the preceding material, the following are somewhat doubtful plants, provisionally referred to *P. dubia,* which deserve future study in connection with the limits of *P. floridana.*

NORTH CAROLINA: Swamp, 1.5 mi. E. of Whiteville, Columbus Co., N. of

Rte. 74-76 (*Schuster and Blomquist* 29228; *Schuster, Blomquist and Bryan* 30001b). SOUTH CAROLINA: Wooded swamp, 8 mi. S. of Bamberg, off U. S. Hwy. 301, Bamberg Co. (*Schuster* 33973, 33982).

I have also seen juvenile material from Florida, attributed to *P. floridana* by Evans (in herb. Yale), which I regard as not safely determinable, from Lena Stein Ravine, 3 mi. NW. of Tallahassee (*Kurz* 9!) and from Cross City (*Kurz* 232!).

Ecology.—In Florida chiefly found in deep, partially evergreen swamp forests, and in rich hammock forests, where the species occurs at the bases of tree trunks and on exposed roots, sometimes on the exposed knees of *Taxodium distichum* (and then barely above the flooding level). Associated are *Ceratolejeunea laete-fusca, Cheilolejeunea rigidula, C. clausa, Lopholejeunea subfusca,* and other Lejeuneae. The species appears confined largely to mesic sites near standing water, where the humidity is permanently high. Less often it is found over coral limestone, and soil over it, along rivers (such as the Hillsborough River, in Florida), associated with *Plagiochila ludoviciana* and *Lejeunea floridana.*

In the few stations situated outside of Florida, found (in *Schuster* 19167a, from near Mt. Olive, Miss.) over damp, shaded ledges, with *Trichomanis petersii, Lejeunea flava* and *Lejeunea* cf. *minutiloba;* and on the bark of *Magnolia grandiflora, in* "Beech-Magnolia" forest along the Big Biloxi River (*Webster and Wilbur* 756), associated with *Metzgeria myriopoda, Rectolejeunea maxonii, Radula caloosiensis* (*cf. langloisii*).

The plant rarely occurs in any quantity, occasionally occurs as scattered plants, which then develop isolated, arching, simple or hardly ramified, leafy aerial shoots. The latter, in drying, have deflexed leaves and become characteristically slender and arcuate. Less often, and only under optimal conditions on the bases of trees in swamps, forming large, olive-green to olive-brown patches (and then frequently fertile). Propagula appear to be developed in almost all collections seen, even though Frye and Clark state "gemmae unknown." The propagula occur both on the postical face of the distal halves of the leaves, and near the posterior margins of the antical (adaxial) faces. The very frequent occurrence of propagula in the latter position appears to be an important systematic criterion, since in our other species it occurs, and there rather rarely, only in *P. dubia* and *P. ludoviciana.*

Differentiation.—*P. floridana* is characterized by an ensemble of characters, of which the most important are: (a) the inability to develop a mod. *laxifolia,* the leaves therefore always being slightly to distinctly imbricate; (b) short decurrent postical and antical leaf-bases; (c) oblong-lingulate, virtually parallel-sided leaves, averaging at least twice as long as broad; (d) propagula usually developed, on both postical and antical leaf-faces; (e) the very diagnostically suberect to oblique orientation of the narrow leaves. The latter criterion gives the plants an aspect that is wholly deviant, only the very closely allied *P. dubia* sharing a similar orientation of the leaves.

P. floridana was confused by Underwood with *P. ludoviciana,* and is compared by its author with this species. However, it differs from it not only in the inferior size, the narrower, hardly ovate-falcate leaves, which are nearly parallel-sided for their distal two-thirds, in their shorter leaf-insertion, with the dorsal base rather short-decurrent, the postical base quite short-decurrent and never strongly reflexed. In the field, furthermore, the fact that the leaves never have the postical margin at more than a 65-75° angle with the stem at once separates this much smaller species from *P. ludoviciana* (in which the postical leaf-margin is characteristically at a right angle with the stem). No close relationship between the two can be hypothesized.

Among our other species, confusion is perhaps possible, on account of the narrow and elongate leaves, with *P. austini,* to which the species is not at all closely related. The two, however, share some features (1) evidently elongate, parallel-sided leaves; (2) short decurrence of postical base; (3) cell form and size; (4) form of the leaf-apex, which is often coarsely bidentate or bilobed; (5) plant size. This superficial similarity has resulted in confusion of the species by Stephani, who determined material of this species as *P. sullivantii* St. (nec Gottsche) (= *P. austini* Evs.), from Sanford, Fla., Rapp, Dec. 1903, NYBG. In spite of the superficial similarities, the two species differ not only in mode of reproduction (leafy propagula in *P. floridana vs.* caducous leaves in *P. austini*), but in color and in the suberect leaves of *P. floridana. P. floridana* also never shows the very strong tendency present in *P. austini* to produce narrow, largely 2-lobed leaves, devoid of accessory teeth, on less robust shoots or branches.

This occasional difficulty in separating the species is clear when such plants as Rapp's material (Sanford, Fla., Dec. 1903) is examined. The mature, robust shoots here bear large leaves, *ca.* 2.25 mm long, which spread at an angle of 65-70° (Fig. 54:5). Although, on the basis of size and spreading of leaves, these might be sought under *P. diffusa,* they lack the obvious border of the leaves of that species, have somewhat ovate-lingulate leaves, with slightly expanded postical bases, and more decurrent antical bases. (In the key in Frye and Clark, such plants would key to *P. smallii* = *diffusa,* on the basis of the robust size, to 4.5 mm wide; however, size here appears to be no criterion.) These specimens possess leafy propagula of both leaf-surfaces — at once eliminating *P. austini* from consideration.

Evans (*loc. cit.,* p. 191) also compares *P. floridana* with *P. dubia* Lindenb. and Gottsche. He states that the former is "near" the latter. *P. dubia,* judging from a specimen from Puerto Rico (Laguna San José, Rio Piedros, Aug. 6, 1937, F. M. Pagan) typically differs in the more robust size, the narrowly, obliquely ovate leaves, whose postical margin is somewhat arched and expanded basally (and thus with the leaves gradually but slightly narrowed distally, rather than nearly parallel-sided), as well as in the smaller marginal teeth, all of which are subequal in size (*i.e.,* none of the leaves shortly bilobed distally). Judging from the drawings in Stephani's unpublished Icones, and from the Pagan specimen, there is little immediate relationship between typical *P. dubia* and *P. floridana.*

However, in the southeastern United States occur plants which appear to represent a small, somewhat impoverished and atypical phase of *P. dubia* (see discussion under the latter). These plants almost fully intergrade with *P. floridana,* and quite confirm the opinion of

Evans about the close affinity of the two taxa. Indeed, prolonged study has not revealed any firm and final criteria which always serve to separate the two taxa, in our area. The retention of *P. floridana* as a species distinct from *P. dubia* is predicated on two assumptions: (a) the constellation of characters of the two species are such that although "individual characters intergrade," the taxa themselves do not wholly intergrade; (b) the regional material referred to *P. dubia* is a small phase, evidently at the northern fringe of distribution of the species, and thus shows what might be termed persistently juvenile features. As is well known, juvenile or impoverished extremes of the various species of *Plagiochila* can hardly be surely separated. Therefore the apparent intergradation may be a superficial, rather than fundamental, transition.

A remote similarity also exists between *P. floridana* and *P. diffusa*. The similarity in leaf-shape and insertion, the relatively short-decurrent postical, and moderately decurrent dorsal leaf-bases, and the similarity in cell-size and in the rather large, occasionally bulging trigones suggest that the two are related. Quite striking is the tendency (noted in the type specimens of both species) for the elongate marginal leaf-cells, especially just below the subapical spinose teeth, to be thick-walled parallel to the leaf-margins, thus forming a more or less discrete border, differing from the interior walls. This is more strongly marked in *P. diffusa* than in *floridana,* as far as has been observed.

In spite of these similarities, *P. floridana* differs in several respects from *P. diffusa,* particularly as follows: the leaves (at least above the shoot-middle) spread at an angle of only 40-45° (usually 50-60, occasionally 65-70° in *P. diffusa*), resulting in a very different facies; the underleaves, though minute, are usually discrete (vestigial in *diffusa*); the plants are less robust, 1.5-2.0, rarely 2.5 to 4.2 mm wide (mostly 4-5 mm wide in *diffusa*); the marginal teeth are less strongly developed, on an average, and usually less than 6-7 cells long x 3-4 (5) cells wide at base, terminated by a uniseriate row of 2-3, rarely 4 cells (in *P. diffusa* with the larger teeth 4-8 (9) cells wide at base x 8-12 cells long, terminated by a uniseriate row of often 4-6, occasionally 6-8 cells). Usually the different angles at which the leaves spread at once serve to separate the two species. Furthermore, *P. floridana* (and the allied *P. dubia*) always have leaves that are slightly to distinctly imbricate, in the moist condition; *i.e.,* the plants are able to form only a mod. *densifolia.* By contrast, all phases of *P. diffusa* seen, including the types of *P. diffusa* and *P. smallii,* are lax-leaved, with the leaves remote when moist; *i.e.,* the species appears to be unable to form anything but the mod. *laxifolia.*

The difficulty in separating the *P. floridana-dubia* complex and *P. diffusa* is demonstrated by the material from Mt. Olive, Miss. (*Schuster* 19167*a;* among *Trichomanis petersii* with *Lejeunea flava, L. minutiloba*). These plants, not very well-developed in most cases, are up to 3.2 mm wide. The leaves spread at an angle of 50-55° with the stem, except on the upper portions of shoots, where the angle may be merely 45°. Much of the material is impoverished, and the leaves then are distinctly less than twice as long as wide,

although mature leaves show the narrowly lingulate form typical of the *P. floridana* complex. A few plants show small propagula of the postical leaf-surface. The cells have very well-developed, mostly bulging, large trigones. The plants of this collection, when first examined, could scarcely be safely referred to *P. floridana*. However, the acute or subacute angle formed by the leaves and stem, on the upper portions of shoots, and the approximate to imbricate leaves, as well as the smaller maximum size (to 3.2 mm wide) all suggest *P. floridana*. Furthermore, the very characteristic border found in *P. diffusa* was not indicated, although the cell-walls of some plants were somewhat evenly thick-walled throughout all of the leaf. The disposition of this material as *P. floridana* therefore appears warranted, considerably extending the range of the species northward to a new limited point.

A further collection, superficially difficult to place between *P. floridana-dubia* and *diffusa* is that of Schuster 22853a; on *Carya*, at Hillsborough State Park. The plants are few and mostly poorly developed, and then show virtually edentate leaves (the apex often, however, bidentate); the most robust plants are only 2.7 mm wide, but show the characteristic leaf-orientation of *P. floridana*, with the leaves at an angle of 45-55°with the stem. These plants also show slight, almost evenly thick-walled marginal cells, but no trace of the peculiar border of *P. diffusa*. The plants again bear scattered few-celled propagula of the leaf-surface — often of the antical leaf surface, and have imbricate leaves, characteristic of *P. floridana*. The antical position of the propagula in this species is also noted elsewhere. I have not seen propagula on the antical surface in any of our other species, except *P. dubia* and *P. ludoviciana*. This position of the propagula may therefore form a further differential characteristic of *P. floridana*. More numerous observations confirming this are, however, needed.

Plagiochila aspleniformis sp. n.
Fig. 56

Quasi similis *P. asplenioidi* et rotundo-subquadratis foliis similibus nonnullis formis *P. asplenioidis;* dissimilis in frequentis terminalibus ramis, in libera adcrescentia propagularum ex inferioribus faciebus foliorum; in parvis cellulis foliorum (generaliter minus quam 23-25 μ latitudine media); in micante structure; in sparse irregularique dentatione rotundo-subtruncatorum folio-apicum.

Plantae mediocres vel magna (cum foliis 3.6-5.5 mm latus), sicca fulgentes, dense caespitosa, flavo-viridis; caules parum furcatum vel simplice; folia caulina patentia, late ovata vel ovato-oblonga, subintegra, apice plus minus truncatis, fere plana, margine postice parum decurrente; amphigastria minuta vel subnulla; cellularum marginalis parietibus aequaliter incrassatis. Typus: Hillsborough River State Park, Hillsborough Co., Florida (*Schuster* 22869), in herb. auct.

In green to *yellowish-green mats* (on coral limestone, on soil, and on sand and at the bases of trees). Shoot system consisting of a prostrate series of primary shoots, and of aerial, simple, once-furcate, or rarely monopodially branched, weakly ascending to loosely decumbent leafy shoots; *branches often furcate and terminal;* leafy shoots robust, 3.6-5.5 mm wide (occasional gemmiparous shoots only 2.6-3.5 mm wide). Plants *strongly shining when dry, often a peculiar yellowish-green* (due to yellowish pigmentation of the cell-walls), and with yellowish-brown to brown stems. Stems *ca.* (225-275) 310-350 μ in diameter, of elongate cortical cells (*ca.* 12-14 μ wide x 46-85, occa-

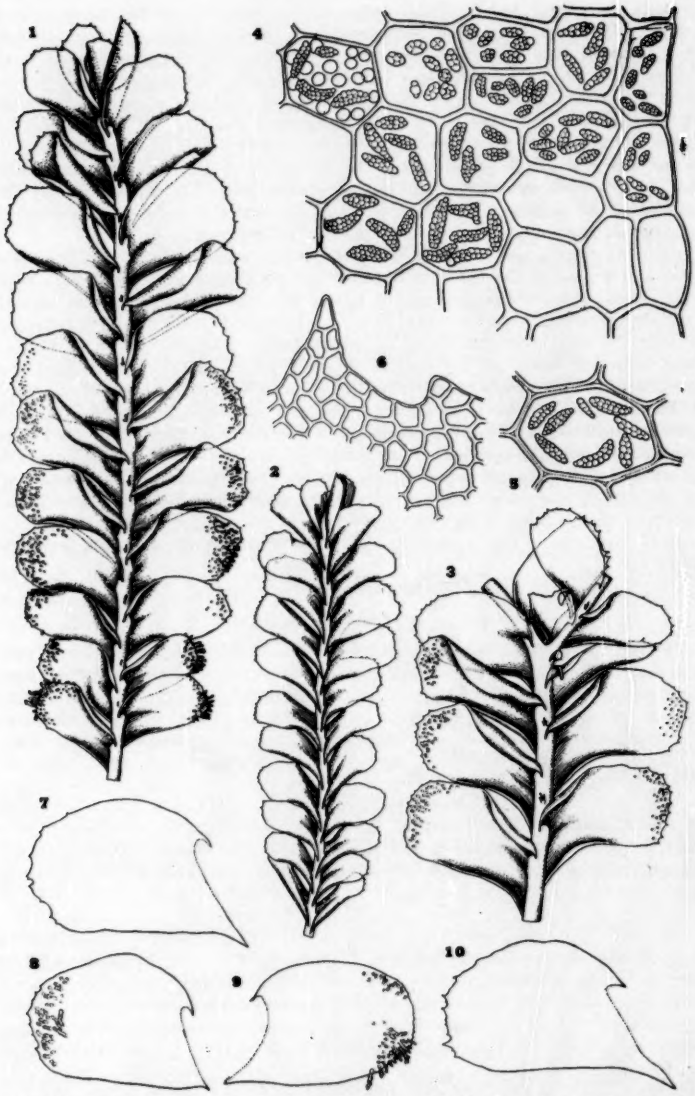

Fig. 56.—*Plagiochila asplenifolmis* Schuster. 1. Mature shoot, with propagula, postical view (x 8.5); 2. Shoot, dorsal aspect (x 5.2); 3. Sector of very robust shoot, postical aspect, showing terminal branch at right, and propagula

sionally 90-100 μ long, strongly thick-walled, with walls often nearly as thick as lumen). Rhizoids absent on leafy aerial shoots. *Leaves contiguous to slightly imbricate, spreading laterally,* not postically secund (but usually *with antical and postical margins deflexed, thus with leaf postically concave*), at *ca.* a 65-75° angle with stem; leaves essentially broadly rounded-rectangular to ovate-rectangular, the *apices usually broadly truncate-rounded,* the *postical margin weakly or scarcely dilated above base,* lying nearly parallel to the antical margin (above the decurrent base), averaging 1700-1900 μ long x 1420-1800 μ wide to 1950-2050 μ long x 1500-1750 μ wide, at times narrower and more nearly ovate-rectangular, with apices broadly rounded rather than truncate (and then *ca.* 2100 μ long x 1670 μ wide), attaining a maximal length of *ca.* 2500 μ x 2000 μ wide; length varying from 1.05 to 1.38 $\times$ the maximal width; antical margin reflexed for most of its length, nearly straight above the moderately decurrent base, entire-margined; postical margin somewhat arched from the *short-decurrent base,* moderately or slightly dilated, *the margin only slightly arched* (and subparallel to antical) above the base, entire or subentire except sometimes on distal one-fourth; *leaf-apex typically subtruncate to rounded-truncate,* occasionally broadly rounded, *bearing usually* 5-10 *small, irregular, relatively inconspicuous, short but broad-based acute or subacute teeth* (1-2, occasionally 3-4 cells long, usually as wide as long); teeth formed of nearly isodiametric cells, the terminal cells 0.8-1.5 $\times$ as long as wide; postical leaf-margin short-decurrent (for up to one-fourth the merophyte length), the postical leaf-bases not closely approximated, *leaving much of the stem visible.* Cells in apical portion of leaf 19-23 x 20-25 (27) μ, in leaf-middle *21-25 μ wide* x 23-30 (33) μ long, in base 19-24 μ wide x 32-44 μ long (not forming a vitta); *cell-walls* $\pm$ *equally thickened, trigones essentially absent* (even under xeric conditions); marginal 2-3 rows of cells (and near postical base a border of 4-6 rows of elongate cells averaging 16-21 x 28-40 μ) *more strongly thick-walled, forming a weakly defined border;* oil-bodies rather *coarsely segmented,* mostly (3) 5-9 per cell, usually fusiform and ellipsoidal (then 3 x 9-13 μ to 3.5 x 6.9 μ, rarely 4 x 12 μ) to subspherical (then 4 μ to 3.5-4 x 4.6 μ); chloroplasts *ca.* 3-3.2 μ. Underleaves inconspicuous, small or minute, but nearly constant, formed of 2-several elongate cilia or ciliate laciniae. Asexual reproduction almost *constantly present, via propagula* produced on the distal fourths of the *postical* leaf surfaces. Habitually sterile.

Type.—Hillsborough R. State Park, Hillsborough Co., Florida (*Schuster* 22869).

Distribution.—Known only from Hillsborough R. in Hillsborough

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(x 8.5); 4. Cells of leaf-margin, with oil-bodies and in upper left cell, chloroplasts (x 465); 5. Cell of leaf-middle, with oil-bodies (x 465); 6. Cells of leaf-apex, with two typical teeth (x 165); 7-10. Leaves, in 8-9, showing the restriction of propagula to distal one-third of the leaves (x 12.5). (Figs. all from *Schuster* 22864, Hillsborough R., Florida.)

State Park, Hillsborough Co., Florida (*Schuster* 22869, 22864, 22863; 33905a, with *P. floridana*) and from near border of Santa Fe. R., in O'Leno State Park, N. of High Springs, Columbia Co., Florida (*Schuster* 37276, 37276a). Both of the stations lie roughly within the so-called "Oligocene Island Area" of central and western Florida.

Ecology.—Frequent on loose, relatively dry, nearly pure sand of low banks or river terraces, there with *Lejeunea floridana, Mitchella repens,* etc.; occasionally also growing up to the fibrous root bases of *Sabal palmetto,* or over coral limestone (then with *Plagiochila ludoviciana, P. floridana, Lejeunea floridana,* etc.). Less often, on sandy banks, *Lejeunea cladogyna* is associated, the Partridge berry, *Mitchella repens,* undergoing ecesis in the *Plagiochila-Lejeunea* mats.

At the second known station for the species, the plants occur under strikingly similar conditions, on loose but damp sand, along low river terraces, again with *Lejeunea floridana!*

Differentiation.—This distinctive species appears to stand isolated among our nearctic species of *Plagiochila.* At first glance, it has the appearance of a disjunct variant or subspecies of the polymorphic *P. asplenioides,* forms of which it superficially resembles. This resemblance is emphasized by the large size (to 5.5 mm wide), the subsimple shoots, the rather distant to approximate ovate-rectangular to oblong leaves that are broadly rounded or rounded-truncate distally, the fine marginal teeth (which, as in *asplenioides,* are absent or vestigial on less robust plants), and the segmented oil-bodies.

However, the plants have several vegetative characteristics that set the species apart from *P. asplenioides,* among them (1) a peculiar yellowish-green, rather pellucid appearance of the leaves, contrasted to the eventually brownish stems; (2) the conspicuous shine of the dry plant (nearly or quite dull in *P. asplenioides*); (3) the leaves, even on the most robust plants, with the marginal teeth few, and mostly near the truncate apex of the leaf; (4) the leaves, even on very robust plants, with no tendency to be postically secund, but spreading laterally. Perhaps more important than the above characters as diagnostic features, are (5) the abundant production on the postical leaf-surface of leafy propagula; (6) the much smaller, non-collenchymatous evenly thick-walled leaf-cells; and (7) the ability to regularly produce terminal branches (Fig. 56:3). In these last characteristics this species differs from the species of the Sectio Asplenioides. The writer suggests that the similarities to this last section are due to superficial resemblances, and do not indicate a close phylogenetic connection. It should be noted, however, that under some conditions, *P. asplenioides* may produce leafy regenerations as described by Douin (1924). His figures are copied by Müller (1942, p. 125, Fig. 8h). In the writer's opinion, the ability, under certain conditions, to produce regenerations from the leaves does not imply that these are produced in nature, and therefore are not strictly comparable to the numerous propagula, freely produced in nature, that characterize *P. aspleniformis.*

In cases of doubt, the stem anatomy alone will separate *P. aspleniformis* from any phase of *P. asplenioides,* since the thick-walled, yel-

lowish cortical cells are narrow and bast-like, ranging from 12-15 μ wide x (45) 60-90 μ long (thus *ca.* 4-8 $\times$ as long as broad!).

In the absence of propagula, it is possible that (if the cell size is not determined) *P. aspleniformis* may be confused with edentate or paucidentate forms of *P. asplenioides*. However, a very considerable gap prevails between the known southernmost range of *P. asplenioides* (northern Georgia and South Carolina) and that of *P. aspleniformis* (ancient Oligocene Island of Florida). The writer suspects that *P. aspleniformis* represents part of the old tropical invasion, which survived in Florida only in the Oligocene Island region during the recent geological periods, and therefore is related most closely to tropical species. To date, no closely similar neotropical species has been found, in which reproduction by leafy propagula is known.

This species keys out near *P. virginica* and *floridana,* with which it shares similar cell-size, and the ability to develop propagula and terminal branches. Its relationships (though distant) appear to be with this complex. However, (1) the somewhat irregular teeth, small in size, and their restriction to the distal one-fourth of the leaf; (2) the equally thick-walled cells; (3) the very short, broadly rounded-oblong leaves all serve to separate *P. aspleniformis* from these two species. The nearly parallel-sided leaf might cause confusion with *P. diffusa,* a quite unrelated species, which also has the relatively small teeth of the leaves restricted normally to the distal one-fourth of the leaf. The exceedingly short-rectangular leaf-form, the slightly imbricate leaves, and the equally thick-walled leaf-cells serve as differential features from *P. diffusa.*

The leaf-cells of this species deserve emphasis. They appear to be virtually equally thick-walled, with at best small, concave, inconspicuous trigones. Under the most mesic conditions that were inhabited by the species (at the type stations), the median cells have relatively thin cell-walls, with minute or small concave trigones. Under the more "typical" conditions (*e. g.,* the site at which the species was most abundant), the plants occurred on loose dry sand some 8-12 feet above the river, on a river terrace — under distinctly xeric conditions. Here the plants had yellowish cell-walls that were evenly thickened (more strongly so in several marginal rows), except for the vestigial trigones which appear to be laid down first. Evidently, this species "behaves" somewhat like *Lophozia bicrenata,* a species unable to produce large trigones, but able to lay down equal layers of wall-thickening. Our other species of the complex lack the ability to develop thick-walled cells, although they may produce large trigones, which may become so large (as in xeromorphic forms of *P. virginica caroliniana*) that they are freely confluent. The behavior-pattern of the cells of this species, in the writer's opinion, is the single most important species criterion since this serves to set the species off from all other nearctic taxa.

The plants appear to be very freely propaguliferous under all conditions. In the few cases where the species was found with other Plagiochilae (*P. floridana, P. ludoviciana*) it was freely propaguliferous,

even though the associated Plagiochilae lacked propagula. Evidently a very slight stimulus is necessary to initiate propagula-formation in this species (even slighter — or at least qualitatively different — than in *P. ludoviciana*).

Sectio IX. HYPNOIDES Carl, emend. Schuster

Robust plants, ± green, dull, usually 3.8-5.5 mm wide, *laxly pseudodichotomously branched;* stems with cortex often brown, 2-3 (4) stratose. Leaves when dry postically secund, the shoots apically also often postically deflexed, especially *when dry, then subcircinate;* leaves notably *flat and laterally spreading when moist, densely imbricate (the ampliate postical bases shingled, hiding the stem)*, rather narrow (usually 1.5-2.2 × as long as wide), ovate-rectangulate to narrowly ovate-falcate, the postical base *distinctly ampliate, not convolute or modified to form a water-sac,* ± *cristate but notably short-decurrent;* postical margin, above base, *usually at nearly right angles with stem;* antical margin slightly concavely arched, reflexed, *long-decurrent;* leaves freely and usually *nearly uniformly spinose-dentate, from the decurrent postical base to the apex* (usually with 16-32 teeth), the antical margin entire, except for 1-2 preapical teeth. Cells strongly collenchymatous, moderate in size, usually 17-23 μ *wide in leaf-middle* and near base; basal cells little elongate, the *leaf not vittate;* oil-bodies usually 4-9 per cell, *distinctly segmented. Underleaves small to large,* usually *of a distinct* (sometimes bifid) *lamella,* armed or resolved into marginal cilia. *Asexual reproduction freely present, by propagula.*

Androecia intercalary, often basal on forks of a dichotomy — thus geminate.

The Sectio Hypnoides was delimited much more broadly by Carl than is done here. Carl (*loc. cit.*, p. 55-57) correctly emphasizes the dense-leaved, strongly distichous facies of the plants of this group. Carl admits that the group is probably closely allied to the Crispatae. He would separate the latter sectio from the Hypnoides on the basis of the more highly differentiated postical leaf-base, which is either cristate or involute. On this basis, *P. ludoviciana* would be referred to the Hypnoides, *P. miradorensis* to the Crispatae. Since these two species are closely allied in most respects, separating them into discrete species groups appears unnatural. A different basis, therefore, must be used in separating the Crispatae and Hypnoides, if this division into two sections is to be maintained. In the opinion of the author, the best grounds for such a division is on the basis of the degree of decurrence of the postical leaf-base. In the short-decurrent species (Sectio Hypnoides), there is no elaboration of a pronounced postical crista, or of a distinct water pocket. This is associated with a notably short decurrence of the ventral leaf-base (usually for *ca.* 0.2 the merophyte length!). Associated with this, the Hypnoides s. str. normally have sharply and nearly uniformly spinose-dentate to spinose-serrate leaves, the dentition being nearly uniform along the postical margin and extending in all cases down to the dilated basal portions of the

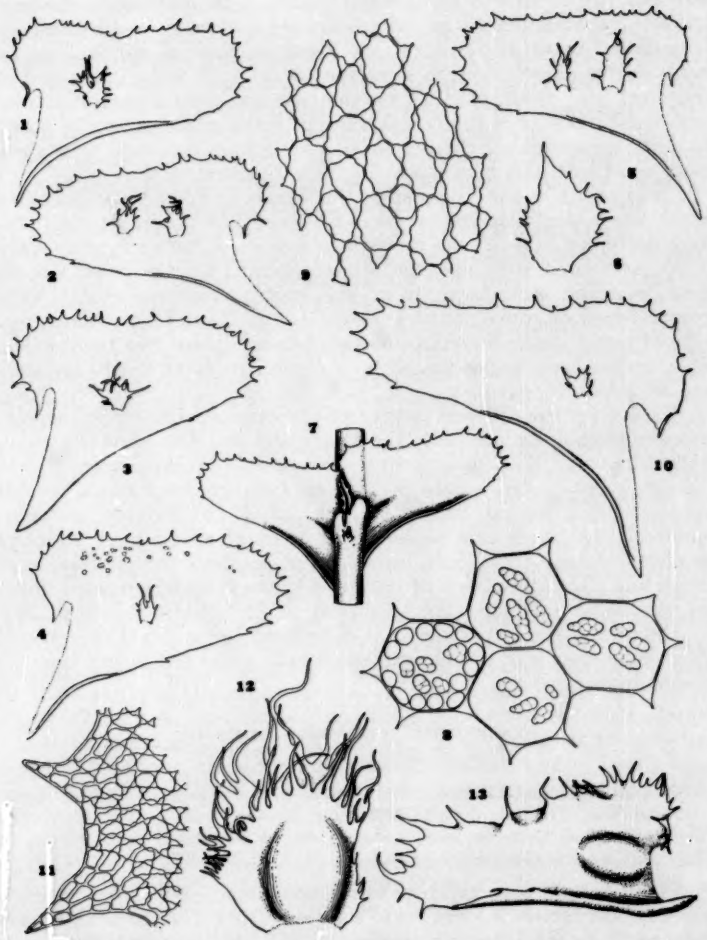

Fig. 57.—*Plagiochila hypnoides* Lindenb. 1-5. Leaves of the most typical and robust Floridian phase, with adjacent underleaves drawn to same scale (x 18); 6. Atypically large underleaf (x 18); 7. Shoot-sector in postical aspect, showing the juxtaposed and cristate postical leaf bases (x 15); 8. Median cells with oil-bodies (x 700); 9. Median cells (x 300); 10. Leaf and underleaf of mod. *megafolia* (x 18); 11. Cells of leaf-apex (x 135); 12. Juvenile perianth, lateral aspect, keel at right (x 24); 13. Female bract (x 18). (Figs. 1-6, 10, drawn to one scale; figs. 1-8, *Schuster* 33801c, Ross Hammock, Fla.; 9-10, Columbia, *Woronow*, ex herb. Th. Herzog; 11-13, *Schuster* 26018, Highlands Hammock, Florida.)

leaf and the decurrent basal strip, usually with undiminished vigor. In the Crispatae there is apparently always a more or less distinct differentiation between the distal and basal portions of the leaf, as regards degree of dentition; in some species (*e. g., P. ludoviciana* and its relatives) the teeth tend to be sharpest and most vigorous distally, with the basal part of the ventral margin entire or subentire; in others (*e.g., P. miradorensis*) the dentition is sometimes restricted to the leaf base, or at least this bears more highly elaborated teeth.

In contrast to the Hypnoides, the Sectio Crispatae (as delimited here) has a long-decurrent postical leaf-base, the decurrent strip running down for 0.5-0.75 the merophyte length, occasionally even 0.85-0.95. Associated with this, the dilated postical base is either sharply erect, standing stiffly away from the stem (forming a *crista*), or is even reflexed or convolute to a higher degree (forming a rudimentary type of *water sac*). No sharp division between these two types is feasible, as has been demonstrated by a careful study of the *P. ludoviciana-miradorensis* complex.

Except for the different degree of elaboration of the postical leaf-bases (and their decurrence), the Hypnoides and Crispatae are essentially identical. Both groups freely produce terminal branches, although ramification is always diffuse; both groups have a notably long-decurrent antical leaf-base; both "tend" to develop geminate androecia, *i.e.*, androecia sessile at the bases of apical bifurcations of leading leafy axes; and both groups regularly show the production of propagula. The distinction of the two sections is further treated under the discussion following the treatment of *P. hypnoides* (see p. 68).

Delimiting the Hypnoides as is done here, the group is represented by a single species in the United States, which has not before been reported from our area.

PLAGIOCHILA HYPNOIDES LINDENB.

Figs. 57-60; 61:6, 9; 62:4-5

Plagiochila hypnoides Lindenb., Spec. Hep. 644, 1844; Carl, Annal. Bryol. Suppl. Vol. II:57, fig. 7, f, 1, 1931.
Plagiochila affinis Gottsche, Mex. Leverm. 154, pl. 8, 1863?
Plagiochila sinuata Gottsche, Mex. Leverm. 151, pl. 9, 1863?

Plants *robust,* deep green to olive-green, nearly dull when dry, the aerial shoots mostly 2-5 cm high, subsimple to 1-2 × pseudodichotomous, erect to suberect, or spreading away from substrate, often somewhat arched or pendulous, (3.2) 4.0-5.5 mm wide. Stems rigid, (240) 260-320 (400) μ in diameter, rarely stouter, yellowish to yellowish-brown with age. Rhizoids few, virtually or quite absent on aerial shoots. Leaves *very densely imbricate,* laterally spreading when moist, postically connivent and secund when dry, *obliquely ovate to ovate-oblong,* (1050-1075) 1100-1175 μ wide at level of postical dilation x (1600-1775) 1900-2150 μ long in our forms (in robust plants to *ca.* 1400-1450 μ wide x 2250-2550 μ long); *length usually* 1.5-1.65 (1.85-2.0) × *the maximal width; leaves short-decurrent postically,* the base

above the *decurrent strip erect, dilated,* 1-*several spinose-dentate,* never forming a water-sac but sometimes narrowly reflexed; *postical base strongly arched and ampliate,* the ampliate bases shingled, with the inner margins erect, *resulting in two lines of vertical, closely juxtaposed spinose-dentate ridges, thus distinctly cristate;* entire postical margin and apex, with ± subequal, sharp, spinose teeth, *usually* (17) 21-26 (32) *teeth per leaf,* of which 1-3 are situated on the apical half of the antical margin; remainder of antical margin sharply reflexed, the *cnemis well developed, the antical base very long decurrent* (the line of leaf-insertion from (850) 950-1200, sometimes 1450 μ long); leaves, except for cristate basal portion, the occasionally sinuous postical margin and the reflexed antical margin, nearly plane; teeth of leaves mostly 3-5 (7-11) cells long, 2-4 cells broad at base, the *apices commonly uniseriate for* 2-3 (4-6) *cells,* the cells usually 20-25 (30) μ x (11) 13-17 μ wide at base. Cells *strongly collenchymatous, trigones large to subconfluent,* the marginal cells often slightly elongated and more thick-walled (otherwise leaves not bordered); subapical and median cells subequal in size, (15-17) 18-21 (23) μ wide x (20) 23-27 (medially often to 32-34) μ long; basal cells near midline of leaf (17) 20-23 (27) x (25) 28-36 (42) μ long; cells near postical leaf-base, along margins, often rectangulate and elongated, 24-35 x 14-16 μ, ± equally thick-walled. Oil-bodies largely 4-6 (8-9) *per cell,* rather *coarsely segmented,* ovoid to ellipsoidal and from 2.5 x 5 to 3-3.5 x 9-10 (rarely 11) μ, occasionally spherical or subspherical and then 4 μ to 4 x 5 μ, to 4-4.5 x 7.5-11 μ, a few to 5 x 7-7.5 μ, composed of *few and coarse, protruding segments;* chloroplasts averaging 4 μ, averaging smaller than oil-bodies. *Underleaves usually distinct throughout,* but often so small as to be seen with difficulty, commonly hidden under the dilated, ampliate leaf-bases, varying usually from 330-450 μ long x 200-350 μ wide (including cilia), but *occasionally very large* in isolated instances, then to 600 μ wide x 1050 μ long or even 750 μ wide x 1350 μ long, the underleaves usually bilobed and variously ciliate, the largest ovate to lanceolate, ciliate on margins. Asexual reproduction via *propagula formed from the postical leaf-surfaces,* usually present in abundance; leaves uniformly persistent.

Dioecious; in our area usually sterile, but occasionally with juvenile perianths. Perichaetial bracts *ca.* 2200-2300 μ long x 1225-1300 μ wide, narrowly oblong-ovate, the postical base rather weakly dilated, the oblong distal half subtruncately terminated; margins with *ca.* 30-36 spinose, strongly variable teeth, the postical base with the teeth often rather crowded, although smaller; base of bracts concave, sheathing perianth-base, the postical margin more or less strongly crispate-undulate. Perianth (juvenile) to 1600 μ long, with cilia, the body then *ca.* 1000 μ long, sharply keeled dorsally (the keel commonly winged and often 1-4-spinose-dentate), inflated basally, complanate apically; mouth oblique, the antical keel longer than the postical, the *mouth longly and rather densely ciliate-laciniate,* the longer cilia 3-4 cells wide at base x 16-24 cells long, a few to 8 cells wide x 32 cells long, tortuous, the apex uniseriate for a length of commonly 9-14

cells. Androecia short, often of only 3-4 (5-6) pairs of bracts, compact, the bracts closely imbricate; androecia commonly situated at bases of terminal forks of leading axes, then *geminate, with vegetative proliferation distally.*

Type.—Brazil (*Willd.*)

Distribution.—A very widespread and polymorphic neotropical species, ranging northward from BRAZIL: S. Paulo, Alto da Serra, leg. F. C. Hoehne, 1920, No. 142, det. Th. Herzog!; Pariti, R. Purno, upper Amazon (Trail, 1874; close to *P. serrata*!); Rio Negro (Spruce Hep. Spruceanae, Amaz. et And. No. 492, as *P. hypnoides* var.), differing in the more copiously ciliate-dentate postical leaf-base, in which it approaches both *P. serrata* and *P. falcato-serrata.* Of two other specimens (NYBG) in the Hep. Spruceanae, Amaz. et And. without number, from "Pará, et fl. Aripecurú" distributed as *P. serrata,* one appears to be typical *P. hypnoides,* the other represents *P. serrata.* PERU: Rio Hualaga, Dept. Soreto (leg. *Killip* 27857, det. Th. Herzog!); COLOMBIA: Florencia, Cagneta (leg. Woronow *No. 59,* det. Th. Herzog!); BOLIVIA: Hac Simaco bei Tipuano, 1400 m. (leg. G. Buchtian, 1920, *No.* 110!; postical leaf-bases long-decurrent, with perianths and propagula; either identical or very close to *P. ludoviciana;* underleaves minute or absent). COSTA RICA: Parismina (*leg. M. Valerio No.* 68!, July 1928; det. et leg. Th. Herzog, 1954); Hamburg Finca, Prov. Lemon (*Standley* 48685, det. Th. Herzog!); Boxuca, "ad Pacific" (*Tonduz* 15663!; extremely large and delicate phase with subentire leaves); COSTA RICA, det. Stephani! SURINAM (*Miquel!*); FRENCH GUIANA: Grant's Rd., Metabon (*Broadway* 888; unusual form with subentire leaves); TRINIDAD (No loc. data, Fendler, 1878-1880!); Blanchisseuse Rd., near St. Patrick Estate (Broadway 7899; phase with small underleaves). JAMAICA (*Wolle!*). PANAMA: prope Villam Crucis, January 1847 (herb. Hooker, NYBG; typical but with rather small underleaves). CUBA: La Prenda, Oriente (leg. *Hioram and Maurel* 2601, 4120!); Sierra de las Yeguas, San Diego de los Baños (*Leon* 5238); Wright, *in* Hep. Cubensis Wrightianae!. PUERTO RICO: Laguna San José, Rio Pedras (*F. M. Pagan* 418!, male); Aibonito (*Pagan* 577! mixed with *P. dubia;* as *"P. ludoviciana"* det. Pagan, Y); Rocky Hill near Pueblito del Rio (*Britton* 9423!; a small mod. *subintegrifolia,* det. as *"P. ludoviciana"* by Evans, Y); Island of Vieques (*Pagan, del Valle and Garcia* 104!); Utado *Pagan* 2170; form with small underleaves!). ST. THOMAS: (*Britton and Marble* 1453); ST. JAN (*Bethania, Britton and Shafer* 360!); and the BAHAMAS: New Providence (*Britton* 253, 3221, 6555; *Brace* 3, 4, 6). The plants from the Bahamas and from the Virgin Islands have been reported as *P. ludoviciana* by Evans (1911, 1918).

Also reported by Gottsche from MEXICO (Jalapa). *P. sinuata* Gottsche, from Zacuapan, Dept. Vera Cruz, Mexico, is, in the author's opinion, probably identical; it differs, according to Gottsche, in the absence of underleaves and the differently shaped leaves. The Mexican *P. affinis* Lindenb. and Gottsche, as figured in Gottsche (1863), also appears to be very closely allied, also lacking underleaves. However, Carl (1931), studying a series of specimens from Costa Rica (leg. Stanley) admits that the degree of development of the underleaves is subject to considerable variation in this complex. As in *P. ludoviciana,* weak forms may lack underleaves almost entirely, while strong individuals may possess them. As a consequence, the degree of development of underleaves (remnants are always to be found!) — or the degree of suppression, cannot, by itself, stand as a species criterion in this complex. Indeed, the material from Colombia (*Woronow* 59, det. Th. Herzog, as *P. hypnoides*)

virtually lacks underleaves on some plants, while in others they are so small that they are easily overlooked.

The plant occurs northward to southern FLORIDA: Ross Hammock, N. of Homestead, Dade Co. (*Schuster* 33801c p.p.); Paradise Key, Everglades Ntl. Park, Dade Co. (*Schuster* 20182a, p.p.; 20150, 20182, 20182a, p.p. with *Radula australis;* 19907, 20180, 20158, 22891, c. androecia; 22606, 20156, 20154; *Small and Lowe* 7029, juvenile!); hammock forest, section 12 of Long Key Pineland, Everglades Ntl. Park, Dade Co. (*Schuster* 22095); deep hammock forest, at E. end of Long Pine Key, Dade Co. (*Schuster* 36827b, 36832; 36832b, with *Lejeunea laetevirens, Rectolejeunea brittoniae;* 36827, with *Rectolejeunea phyllobola;* 36827a, with *Mastigolejeunea auriculata*); deep Mahogany Hammock, 2.5-3 mi. W. of "SW. bend of Ingraham Hwy." just SW. of end of Long Pine Key, Everglades of W. Dade Co. (*Schuster* 37301e, 37326b, 37323d, 37308a, 37308d; 37308g, with *Neckera disticha;* 37369b, 37336b, 38328c, 37321,, 37368a, 37368, 37341, 37366b, 37342c, 37355d, 37366a, 37358a, 37357, 37366, 37352a); Royal Palm Hammock, Collier-Seminole State Park, Collier Co. (*Schuster* 26130, 20420, 20415, 20412a, 20282, 20421, 20295a, 20270a, 26132b); Highlands Hammock State Park, 6 mi. W. of Sebring, Highlands Co. (*Schuster* 19942, 26018, c. per juv.; 19954d, 20111, 20092, 26015, 26016, 26014a, 26024a); Mathesson Hammock, Old Cutler Rd., Dade Co. (*Schuster* 22688, 22681, 22690); Timm's Hammock, N. of Homestead on Bauer Drive, Dade Co. (*Schuster* 22851, 22857b); Costello Hammock, near Silver Palm, Dade Co. (*Schuster* 22964b); Freeman Hammock, Arch Creek Prairie, Dade Co. (*Small, Mosier and Small* 6145!); in Everglades near Camp Longview (*Small and Wilson* 1545*a*!; male); Hammocks near the Homestead Trail, near Camp Longview (*Small and Wilson* 2051, 2059!); near Homestead Road, between Cutler and Longview Camp (*Small and Carter* 1370 p.p.!); Elliott's Key, Monroe Co. (*Small and Nash* 468!; form with unusually small underleaves); Timm's Hammock, Dade Co. (*Small and Mosier* 5290a; *Small, Mosier and Small* 6981!); Nixon-Lewis Hammock, Dade Co. (*Small and Mosier* 5246 p.p.!); *Paurotis* Hammock, on Cape Sable, Monroe Co. (W. S. Phillips herb. *No.* 115); Deep Lake, Collier Co., on *Acer rubrum* (W. S. Phillips herb. *No.* 46!). In addition, two collections of somewhat juvenile plants appear to belong here: Palma Vista Hammock, near Paradise Key, Dade Co. (*Schuster* 22148); Brogdon Hammock, Dade Co. (*Small and Mosier* 6232; determined, with question, as *P. floridana* by Evans); Redlands Hammock, Kings Hwy., NW. of Homestead, Dade Co. (*Schuster* 42129a, 42119a).

Very rarely occurring northward to central Florida, where apparently localized in the eastern edge of the Oligocene Island region: near Oviedo (*Rapp* 85!, p. min. p., among *P. floridana,* Y); on rotten logs, 10 mi. S. of Sanford, Seminole Co. (*W. L. Dix,* March 1950!; det. by Evans as *"P. ludoviciana,"* in herb. Y; the plants are a typical, if rather small, phase and bear androecia; the androecia in part geminate and fasciculate, with innovations from just below or even within the androecium that are immediately androecial); Big Tree County Park, 3 mi. N. of Fern Park, Seminole Co. (*Schuster* 42178, 42179a).

Except for the isolated collections from Highlands and Seminole Counties the species appears restricted to the Everglades of southern Florida. It was previously unknown from the United States, although numerous previous collections had been made, almost all misdetermined for *P. ludoviciana.*

Ecology.—A widespread species, usually at the bases of trees or on fallen lianas or logs, usually in deep evergreen forests; also fre-

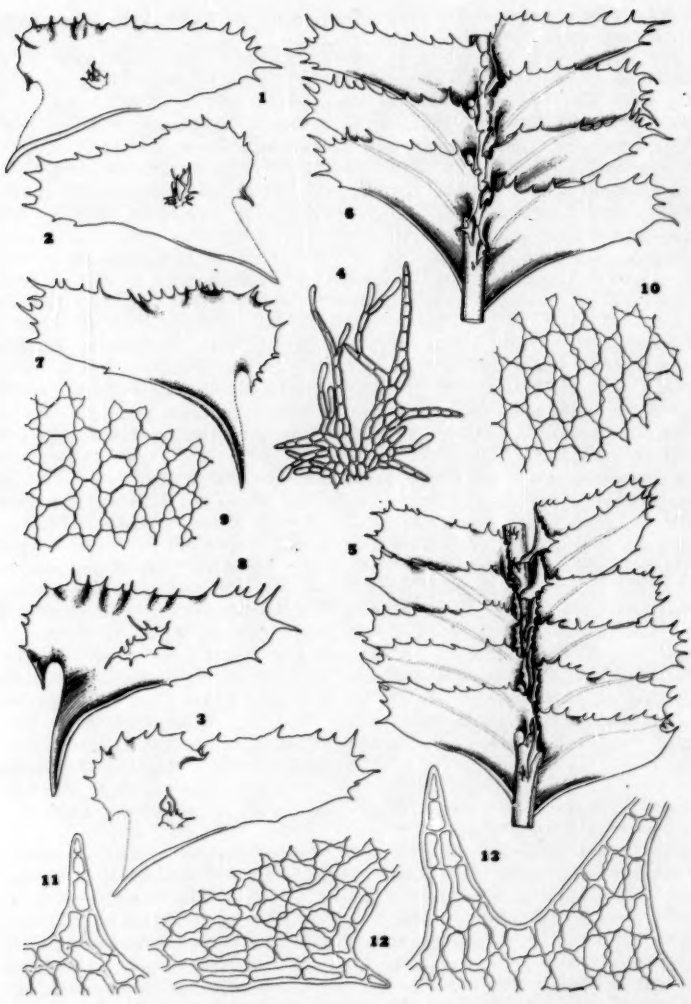

Fig. 58.—*Plagiochila hypnoides* Lindenb. 1-3. Leaves and underleaves (x 16); 4. Underleaf from fig. 2 (x 80); 5. Shoot-sector of robust phase, postical aspect (x 11); 6. Shoot-sector of phase with largely vestigial underleaves (x 17); 7-8. Two leaves and underleaf (x 13); 9. Basal cells (x 190); 10. Median cells (x 190); 11. Tooth of postical margin (x 190); 12. Tooth near base of postical margin (x 190); 13. Cells at leaf-apex (x 190). (Figs. 1-5, *Schuster* 20182, Paradise Key, Fla.; 6-13, *Schuster* 19954d, Highlands Hammock, Fla.)

quently forming festoons on twigs and small branches. The local plants at the bases of tree trunks, associated with various Lejeuneae (*Lejeunea longifissa, L. minutiloba, L. glaucescens, Ceratolejeunea laetefusca, Cololejeunea diaphana* and *contractiloba*), *Radula australis,* and such mosses as *Neckera disticha.*

Perhaps more common high on tree trunks of a variety of trees. For instance, on *Quercus virginiana,* together with *Ceratolejeunea laete-fusca, Cheilolejeunea rigidula, Mastigolejeunea auriculata* (*Schuster* 19954d), or on bark of *Persea borbonia,* with *Frullania squarrosa, Mastigolejeunea auriculata* (*Schuster* 26132b), on bark of *Exothea paniculata* (with *Radula australis, Cheilolejeunea clausa, C. rigidula, Lejeunea laetevirens* and *bullata, Mastigolejeunea auriculata*) and also on bark of *Citharexylum fruticosum, Carya* sp., and *Laurocerasus.* In addition to the preceding hepatics, there are also associated *Lopholejeunea subfusca,* rarely *Frullania riojaneirensis,* and a series of other Hepaticae (*Cheilolejeunea clausa, Ceratolejeunea cubensis, Lejeunea glaucescens, Cheilolejeunea decidua, Taxilejeunea* sp.) and mosses (*Neckera undulata*). The species also occasionally occurs at tree-bases (as on *Elaphrium simaruba*), with *Radula australis, Lejeunea laetevirens,* etc., forming the matrix in which the fern *Campyloneurum phyllitidis* undergoes ecesis.

In the southern tip of Florida occasionally, in dense hammocks, forming weak festoons on twigs and small branches; then often with *Radula australis,* or with *Caudalejeunea lehmanniana.*

Variation and Differentiation.—A polymorphic taxon, to which will probably be referred, on careful study of the neotropical representatives of the group, a whole series of recently proposed "species." Reference has already been made to the fact that, particularly with variation in robustness, there is considerable variation in the size of the underleaves; in extreme cases they may be almost obsolete. The regional collection, (*Schuster* 33801c), is "typical" in that the underleaves are rather large and easily observed, *if* the ampliate leaf-bases are pushed away from the stem (Fig. 59:4-5); by contrast, the rather robust and well-developed plants of *Schuster* 19954d, in some cases (Fig. 58:6) may show virtually underleaf-free stems, while other stems of the same collection may possess rather large and obvious underleaves (Fig. 58:8); the great disparity in degree of development of underleaves within the same small patch of plants suggests this character has been much overemphasized as a systematic criterion.

If the degree of variation in leaf-shape and in dentition in the allied *P. ludoviciana* may serve as a criterion, we can expect to find a wide range in degree of development (or suppression) of dentition in this species. Some of the extremes have surely been described as different species. Carl (1931, p. 57) also entertains this opinion, stating: "Vielleicht müssen noch andere Arten zu *P. hypnoides* gestellt werden, wenn die Variationsbreite dieser offenbar vielgestaltigen Art Berücksichtigung findet." The variation in leaf-shape of this species appears to be somewhat different from that occurring in

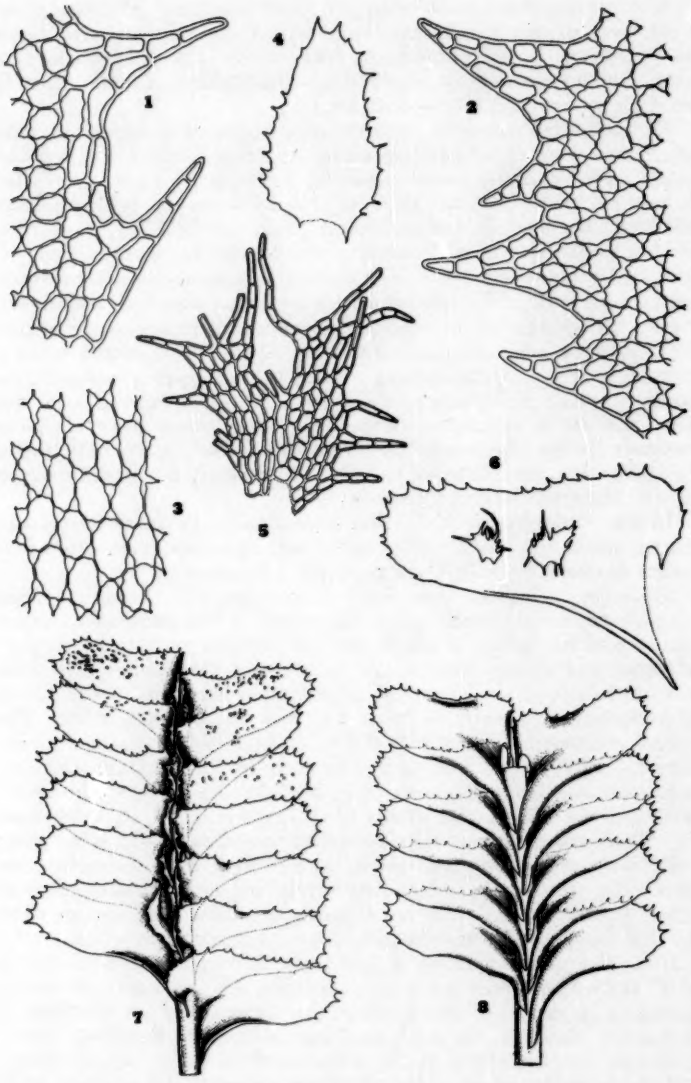

Fig. 59.—*Plagiochila hypnoides* Lindenb. 1. Cells from postical leaf-base above decurrent portion, showing typical dentition (x 240); 2. Cells of leaf-apex (x 240); 3. Median cells (x 240); 4. Extremely large, atypical underleaf (x 21.5); 5. Normal underleaf (x 115); 6. Leaf and, to same scale, two under-

the closely allied *P. ludoviciana*. The leaves are always narrow and elongate, with the length from a minimum of 1.4 to a maximum of 1.9, rarely 2.0 × the width at the widest point of the ampliate base. They always possess at least 1-2 spinose teeth just above the short-decurrent postical strip, and most often bear 1-several spinose teeth even on the decurrent strip. The teeth are always well developed, at least in our phases, and usually show little or no differentiation between the subapical and apical as regards size. However, occasionally (*Schuster* 19954d; Fig. 58:6-8) the teeth are notably coarser, and the apical may be sharply spinose, the leaf-apices becoming more nearly lacerate-laciniate.

With our present knowledge, *P. hypnoides* is restricted to plants with three critical features that, taken as a whole, serve to separate it from other regional Plagiochilae: (a) the leaf-margins, from the commonly narrowly subtruncate apex to the ampliate and decurrent postical base, are sharply and rather regularly spinose-dentate; (b) the distinctly ampliate anu spinose-dentate postical base is short-decurrent, with formation of a vestigial crista — and never of a water-sac; (c) ciliate-dentate underleaves, even if vestigial ones, are present.

In the short-decurrent postical leaf-bases which are never broadly reflexed, *P. hypnoides* is, at least in theory, sharply separable from the otherwise very similar *P. ludoviciana*. In actual practice, this distinction is often difficult to maintain. However, it seems evident that the difficult transitional forms probably all represent weakly developed phases of *P. ludoviciana*. As a consequence, it must constantly be kept in mind that all short-decurrent, spinose-dentate, dense-leaved Plagiochilae occurring in the southeast cannot automatically be referred to *P. hypnoides*. In most respects, these two species are extraordinarily similar. Indeed, in antical aspect, the two are often nearly inseparable. Both species abundantly produce slender leafy propagula from the postical leaf faces, and both have leaf-cells and segmented oil-bodies with essentially identical dimensions. In both *P. hypnoides* and *P. ludoviciana* there is a similar response in the living plant to drying: the leaves become ± strongly postically secund and connivent, and the shoot becomes postically arched and curved, although hardly circinate. As a consequence, dry plants commonly appear very narrow, and quite linear, in antical profile.

The regional plants, as is so common with our other Plagiochilae of tropical derivation, are somewhat smaller than the material from the tropics which I have had occasion to study. They are mostly 3-3.5 mm wide, less often (*Schuster* 19954d, 20092, 20182) to 4.4-5.0 mm wide; well-developed plants from the tropics may be 5.0-5.5 mm wide or more. Except for this, they match almost perfectly, in all respects, such plants of *P. hypnoides* as those from Costa Rica (*Standley* 48685) and from Colombia (*Woronow* 59). One characteristic, in particular, equally developed in all collections of *P. hypnoides* seen,

leaves (x 21.5); 7. Shoot-sector, with propagula, postical aspect (x 12.5); 8. Shoot-sector, antical aspect (x 12.5). (All from *Schuster* 33801c, Ross Hammock, Fla.)

deserves emphasis. Although the postical leaf-base is short-decurrent, the postical, ampliate base is somewhat reflexed-circinate due to its curved line of insertion, forming a postically open, in extreme cases ± conical basal pocket, although not a water-sac or crista in the strict sense.

Almost all of the regional plants studied were sterile, but bore an abundance of filiform, slender propagula. In two collections (*Schuster* 26018, 20092) immature perianths were developed. The female bracts seen were more oblong and narrower than those commonly found in *P. ludoviciana* (compare Figs. 57:13 and 61:3). They also were more sharply spinose-dentate or even laciniate-dentate, with the postical bases freely dentiferous. With study of a series of gynoecia, these differences largely disappear. In *P. ludoviciana,* the most spinose-leaved and attenuate-leaved forms (Fig. 64) have bracts that are as narrow and elongate, and are almost equally copiously dentate basally (Fig. 64:2-3). The immature perianths showed a great similarity to those of *P. ludoviciana.* The antical keel was similarly elongated, and was either in the form of a vestigial narrow lamella or was broader and bore 1-several small teeth near the base (Fig. 57:12). The postical keel was similarly abbreviated, with the consequence that the mouth was distinctly oblique. The very great degree of variation in development of the cilia in *P. ludoviciana* is clear from the figures (Figs. 61:2; 64:7; 62:2; 65:3-4); it probably will be found to include that of *P. hypnoides.* However, the few perianths of *P. hypnoides* seen (Fig. 57:12) differ in one respect: the cilia are longer and more tortuous. Several collections (*e.g., Schuster* 22891) have also been seen with androecia. These are short, often of only 3-4 pairs of bracts, compact, and often situated at the bases of furcate branches (thus geminate); they always proliferate vegetatively distally.

Juvenile forms of *P. hypnoides,* in which the aerial stems are short and simple, are frequent in our area. These may be virtually impossible to recognize, since they often do not show the marked shingling of the leaves characteristic of mature plants. Such plants may be confused with members of the Contiguae. However, prolonged search will generally reveal at least a few lamellate underleaves (Fig. 60:2, 4) that are suggestive of those of more "normal" *P. hypnoides.*

To our south, *P. hypnoides* becomes a more problematical taxon than within the immediate region here treated, since a number of very closely allied species inhabit the neotropics. The most immediately allied are, perhaps, *P. serrata* (Roth) G. L. et N., and *P. falcato-serrata* Carl ex Herzog. Both of these species have the postical leaf-bases more sharply and conspicuously ciliate-dentate, and *P. falcato-serrata,* in addition, has a basally more conspicuously ampliate leaf. From the restricted material of *P. serrata* available, it seems possible that *P. hypnoides* and *P. serrata* represent the extremes of a single variable taxon. However, no plants showing a clear-cut approach to *P. serrata* have been seen from our region.

P. serrata, in some respects, serves to connect the Hypnoides with the Crispatae. In at least the robust extremes of this species (*e.g., Richards* 827, British Guiana, near Akaio Landing, Cuyuni R.) the decurrence of the leaves ranges up to about 0.35-0.4 the merophyte length. However, in the Brazilian plants distributed by Spruce (Hep. Amaz. et And.: Para et fl. Aripecuru) the decurrence is perhaps only 0.25-0.3 the merophyte length. In both of these collections the leaves

are more narrow and drawn out than in the more ovate-triangular leaved *P. hypnoides*, and the dilation of the postical base is considerably less marked. As a consequence, the stem, in postical aspect, is not totally obscured by the leaves. Whether these differences are constant remains to be established. In any case, the more sharply spinose-dentate postical base will, in general, serve to separate *P. serrata* from

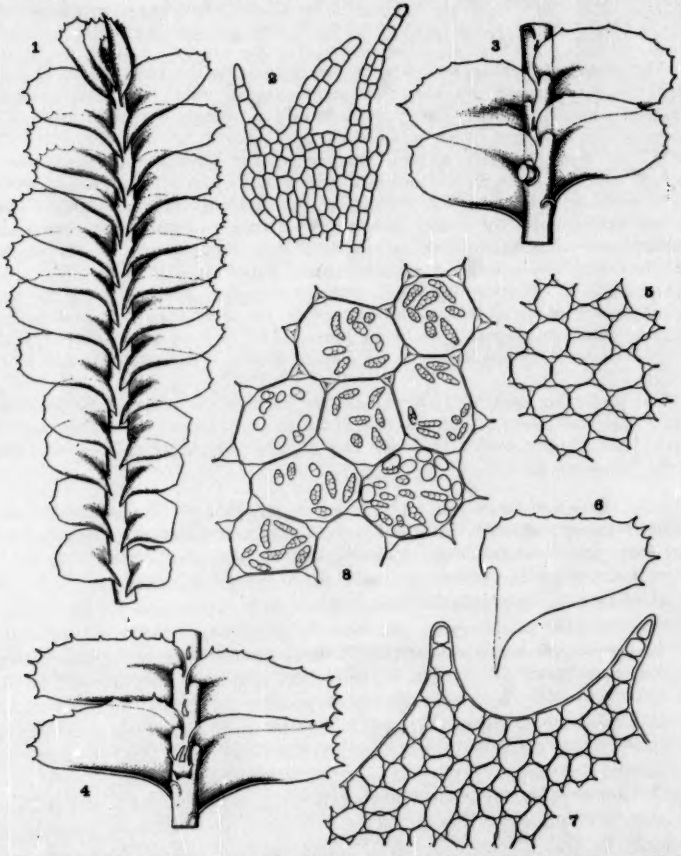

Fig. 60.—*Plagiochila hypnoides* Lindenb., juvenile extreme, with superficial "intergradation" to *P. virginica*. 1. Shoot, antical aspect (x 13.5); 2. Large underleaf (x 100); 3. Juvenile shoot-sector, postical aspect (x 18); 4. Shoot-sector, more nearly mature, postical aspect (x 16.5); 5. Median cells (x 190); 6. Leaf (x 18); 7. Apical cells (x 190). *Plagiochila virginica* Evs. 8. Median cells, with oil-bodies and in lower right, chloroplasts (x 460). (Figs. 1-7 from plants collected at Brogdon Hammock, Fla., *Small;* 8. Unicoi Gap, Georgia, *Schuster;* see in Fig. 44.)

P. hypnoides, although the number of teeth varies. For example, there are only 2-3 subbasal teeth in the aforementioned Brazilian plants of *P. serrata;* these, however, are much sharper and more prominent than in *P. hypnoides.* In the Brazilian plants the leaves are also more strongly falcate and curved, with a more concavely arcuate antical margin than in *P. hypnoides.* The British Guiana plants cited above do not show as distinctly falcate a leaf-form, however, although the leaves remain nearly as narrow as in the Brazilian plants.

The plants of *P. thysanotis* Spruce (as typified by the Hep. Amaz. et And., from the Rio Negro) are also very significant in fixing the limits between Hypnoides and Crispatae. These plants have the strongly narrowed and falcate leaves of the Brazilian plants referred by Spruce to *P. serrata;* they have similarly, but more strongly spinose margins; particularly the postical base is strongly spinose-ciliate with about 4-5 curved and often reflexed, tapering ciliiform teeth occurring on the margin of the postical decurrent strip. These plants, furthermore, have the decurrence relatively strongly developed, the crispate and cristate, spinose-ciliate postical strip being decurrent for at least 0.5 the merophyte length on mature leaves. Stephani (1905, p. 507) places *P. thysanotis* in synonymy under *P. serrata;* the plant may be a robust, maximally dentate phase of this species. However, the more decurrent postical base suggests that two species may be at hand. The lack of other than vestigial underleaves in *P. thysanotis,* even on mature shoots, is a notable feature of the species.

The preceding study of *P. hypnoides* and its relatives suggests that, together with *P. falcato-serrata,* a difficult complex is at hand whose comprehension will require much more work. The four related taxa may be tentatively separated by the following key:

1. Leaves narrowly ovate-triangular, not strongly falcate, the postical base rather strongly dilated, with (0) 1-3 relatively small teeth; underleaves, at least on robust and mature shoots, discrete and often very large, dentate but not longly ciliate. ..... *P. hypnoides*

1. Leaves lingulate-triangular to lingulate-falcate. 2

2. Leaves with postical base not strongly ampliate, the straight postical margin simply rounded gradually into the postical decurrent strip; postical base sparingly dentate to ciliate-dentate, with only 3-5 teeth of decurrent strip. 3

3. Underleaves distinct; postical base only 0.25-0.35 (0.4) decurrent, the decurrent strip with 2-3 spinose but relatively small teeth. ..... *P. serrata*

3. Underleaves vestigial; postical base *ca.* 0.5 decurrent, the very conspicuous, crispate and cristate decurrent strip armed with 3-4 (5) long and curved, spinose-ciliate teeth. ..... *P. thysanotis*

2. Leaves with postical base very markedly ampliate, strongly arched; postical decurrent strip curved, closely toothed with spinose teeth; underleaves large, lamellate, densely ciliate. ..... *P. falcato-serrata*

A study of the preceding species, and of the closely allied *P. cristata,* suggests that these species, all indubitably belonging to the Hypnoides, are separable from the Crispatae chiefly on the basis of the tendency for sharp dentition of the postical leaf-bases, coupled with

a tendency for the decurrence to be markedly shorter. In none of these species does the decurrence ever appear to exceed 0.5 the merophyte length; in the Crispatae it rarely is as low as 0.5 the merophyte length, and the postical base is either edentate or virtually so or else provided with only 2-3 very small teeth (*e.g.*, in *P. miradorensis*). There is another associated tendency in the Hypnoides, which holds for all but exceptional species such as *P. blepharobasis*: the leaf-margins "tend" to be rather uniformly serrate to spinose-dentate from the base to the apex. Only in *P. blepharobasis* is the dentition reduced distally, with the Hypnoides-like dentition confined to the short-decurrent base (see Herzog, 1932, Fig. 9a-b). Finally, in the Hypnoides we find a marked tendency for the underleaves to be lamellate, the base being formed by a marked, sometimes 2-4-lobed and crispate lamella, the margins more or less ciliate. Such underleaves are typical of *P. hypnoides, P. falcato-serrata, P. blepharostoma, P. serrata,* etc. It is only very rarely that the underleaves are strongly reduced (*i.a.*, in *P. thysanotis* and *P. hoehni* Herzog — see Herzog, 1932, p. 220, Fig. 11g-i). By contrast, the Crispatae normally possess underleaves that are divided into narrow laciniae or cilia, either virtually to the base or to within one-fourth of it; they also often show marked reduction of the underleaves, and such typical members as *P. perbella* Herz. (Herzog, 1952, p. 77, Figs. 10-11) are described as with the underleaves "omnino nulla," although vestigial underleaves surely must occur.

Section X. CRISPATAE Carl

Plants *relatively robust,* 2.5-4.5 (5.5) mm wide x 2-8 cm long, spreading from substrate and often pendulous or forming festoons, light green to olive-green or olive-brown, the stems often brown, *dull* or nearly so. Branching of weak plants sporadic, in large part monopodial and intercalary, but *robust plants sparingly and distantly to copiously furcate, terminally branched;* gynoecia regularly with 1-2 innovations. Stems robust, over 220-400 μ in diameter, over 12 cells high; cortex 2-3 stratose. Leaves typically very *densely imbricate, ovate-triangular to ovate-falcate in shape, ampliate, ca.* (1.3) 1.6-2.35 $\times$ as long as wide; postical leaf-margin showing a well-defined tendency to be undulate or crispate (at least on the bracts and subfloral leaves of female plants), with *postical base long-decurrent* (usually *ca.* 0.5-0.8 the merophyte length), *the decurrent strip erect, and crest-like, or reflexed and forming a postical pocket; leaf long-decurrent antically,* forming a sublinear, oblique fold. Cells $\pm$ strongly collenchymatous, *medium sized* (18-23 μ wide in leaf-middle); *basal vitta absent;* trigones large to bulging (only mod. *meso-* and *pachyderma* normally occurring in nature); oil-bodies 4-9 usually, up to 5.5 x 9 μ, coarsely to finely segmented, appearing *coarsely papillose. Underleaves distinct, large,* less often nearly obsolete, *divided into cilia or laciniae. Asexual reproduction by means of leafy propagula of the postical* (and more rarely also antical) *surface of the persistent leaves.*

Plants *frequently producing perianths,* but apparently rarely androecia. Perianths inflated below, distally compressed, the long dorsal keel 2-3 mm long, *usually much longer than the postical keel, the mouth thus* (in lateral view) *obliquely truncate, very broad,* often reflexed in part, *ciliate to ciliate-laciniate; dorsal keel usually at least narrowly winged,* sometimes dentate, postical keel apparently never winged. Androecia either terminal on leading shoots and becoming intercalary, or *often basal on the dichotomous forks of a leading* axis, the bracts closely imbricate, forming a compactly spicate androecium, similar to leaves in degree of postical decurrence and in the dentition of the margins, their basal 0.5-0.7 strongly concave, forming a conspicuous basal pocket.

This section, in the very long-decurrent postical crest-like or reflexed leaf-bases, occupies an isolated position. The more advanced species (*P. undata, P. miradorensis*) show no close relationship to other sections, but the less advanced (*P. ludoviciana*) often show much lesser development of the postical reflexed decurrent strip, and then clearly show a close relationship to the species of the previous section. Confusion with species of other sections is hardly possible, although juvenile plants may approach mature plants of the Sectio Contiguae. The separation of species of this section from those of the preceding (Sectio Hypnoides Carl) is often difficult. *P. ludoviciana,* a crista-bearing species, would go into the Hypnoides if we follow the concepts of Herzog (1932), even though placed as a primitive species of the Crispatae by the writer. Herzog (*loc. cit.,* p. 217) considers the two sections closely affined, stating "Es ist mir überhaupt sehr wahrscheinlich, dass Crispatae und Hypnoides eng zusammengehören." The writer suggests that species with a long-decurrent postical leaf-base (forming a sharp crista- or water-sac) be assigned to the Crispatae; species with a short-decurrent postical base, at best narrowly reflexed, are referred to the Hypnoides (see pp. 56, 68).

Herzog (*loc. cit.*) assigns such species as *P. undulifolia* to the Hypnoides; this species, as far as I can judge, is scarcely separable from our common *P. ludoviciana.* Similarly, *P. blepharobasis,* identical in leaf-form, in the virtually edentate margins, except for the short decurrence of the reflexed base, to *P. miradorensis* is placed in the Hypnoides, "oder vermittelt zwischen diesen und den "Crispatae" (Herzog).

The North American species of the Crispatae, and of the allied Hypnoides, have been extraordinarily confused in all the preceding literature. Twelve different species, mostly quite unrelated, have been found in herbaria (and in the literature) listed as *"P. ludoviciana."* Inversely, good material of *P. ludoviciana* has been listed under several other names, as for instance, *P. undata* (Redfearn, 1952). Fully 75 percent of all herbarium specimens (and literature reports) of *"P. ludoviciana"* which have been seen refer to other species. Prominent among the misunderstood related species are *P. miradorensis* and *P. hypnoides,* which have not been previously reported from the United States, and *P. undata.* The latter species is so distinct that no reason exists to devote a discussion to its affinities and distinction. *P. hypnoides* also is nor-

mally easily distinguished. However, *P. ludoviciana* and *P. miradorensis* are closely allied, exhibiting variations which to some degree bridge the distinctions between them. The following essay on the variability of the *P. ludoviciana-miradorensis* complex, based on a three-month study of all accessible material, serves to elaborate some of the features in which these species approach each other, and to suggest points of distinction.

In addition to the great latitude of variation which the regional material exhibits, there is superimposed a bewilderingly wide amplitude of variation in the tropical members of the *P. ludoviciana-guilleminiana* complex. The concept of species limits here is fluid, needing to be hardened through extensive field experience and experimental work. Some of these problems are briefly discussed under *P. ludoviciana* (pp. 89-94). The immediately subjoined discussion is restricted to the members of the complex occurring in our immediate area.

Variation.—*P. ludoviciana* and *P. miradorensis*, as broadly delimited here, exhibit an extraordinary polymorphism. It is possible that several additional, closely allied species are involved. This appears to have been the conclusion of Gottsche (1863), who described a large number of "species" in this complex. However, as soon as a detailed analysis is made of a long series of specimens, the differences that initially appear so impressive almost disappear. Of more importance, systematically, is the fact that there is little or no linkage in the appearance of particular characteristics — each individual feature varying to a large extent independent of the others. As a consequence, if species are to be recognized at all in this complex, we must limit them to the two here recognized, or we would have to recognize infinitely more than the nine or ten "species" recognized in this complex by Gottsche for Mexico.

The polymorphism of *P. ludoviciana* and *P. miradorensis* occurs along a series of lines, including (a) variation in degree of decurrence of the postical leaf-base; (b) variation in leaf-shape; (c) variation in dentition; (d) variation in the form of the crista or of the "water-sac"; (e) variation in cell form and size; (f) variation in propagula formation; (g) variation in form of the ♀ bracts; (h) variation in form and dentition of the perianth; (i) variation in degree of development of the underleaves. The following analysis serves to document this polymorphism. It is to be noted that this analysis is based almost exclusively on regional material.

Variation in degree of decurrence of postical base[1]:— In all typical material of *P. ludoviciana*, the postical base is long-decurrent (0.6-0.75 the merophyte length, normally), the decurrent strip extending down (from the arched summit of the line of insertion) for a distance equivalent to 0.55-0.75 the length of the degree of decurrence of the antical half (again measured from the summit of the arched portion of the line of insertion) (Figs. 61:7; 62:1, 10). The antical half of the leaf is prominently long-decurrent (the line of insertion running

[1] Figs. 61-63 are intended to portray much of the gamut of variation in this complex, and should be referred to in this conjunction.

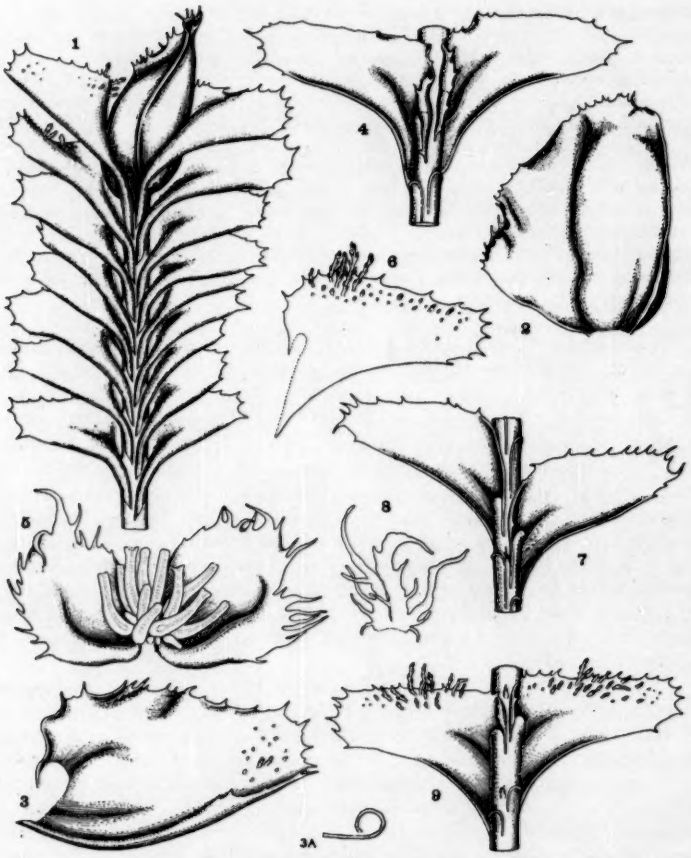

Fig. 61.—Sectios Hypnoides and Crispatae. 1-3, 7-8, *P. ludoviciana* Sulliv. 1. Shoot with perianth, with few propagula of adaxial leaf- and bract-surfaces (x 14); 2. Perianth, lateral aspect, keel at right (x 18); 3. Bract, abaxial aspect (x 18); 3A, the "cnemis," in cross-section, showing the strongly involute leaf-margin; 7. Shoot-sector, postical aspect, of mod. *angustifolia-dentata*. showing crista and postical decurrence (x 16); 8. Underleaf of maximal size (*ca.* 30). 4, 5. *P. miradorensis* Gottsche. 4. Shoot-sector, postical aspect, showing convolute postical leaf-bases and decurrence (x 16); 5. Juvenile perianth, atypical, opened to show archegonia. 6, 9. *P. hypnoides* Lindenb. 6. Leaf with propagula, postical aspect (x 14.5); 9. Shoot-sector, with propagula, postical aspect, showing crista and short decurrence (x 16). (Figs. 1-3, near Chunchulla, Alabama, *Schuster* A-109; 4-5, NW. of Brooksville, Fla., *Schuster* 22075a; 6, 9, Paradise Key, Florida, *Schuster* 20295a; 7, *Schuster* 22975.)

down for a distance of *ca.* 760-950, occasionally 1050-1100 μ; this line equal to *ca.* 0.8-1.0, the maximal leaf-width just above the base). As a consequence the degree of decurrence of the postical base varies from *ca.* 475-575 μ. However, in weak forms, or on weak stems, the degree of decurrence may be much less, and such relatively short-decurrent, juvenile manifestations may approach *P. hypnoides* in this respect. The adult phases of these two species, however, differ greatly in the degree of decurrence (compare, *e.g.,* Fig. 61:7 and 9). Some of the considerable confusion existing in the *P. ludoviciana - guilleminiana* complex is attributable to the variation in degree of decurrence that exists between normal or optimal forms of the same species, and between small plants exhibiting juvenile features. Often differences are exhibited on individual stems that are suggestive: the lower, more juvenile leaves showing a lesser degree of decurrence than the upper, normal leaves. As a consequence, observations need to be restricted to mature, normal portions of leading stems or main branches, on which *P. ludoviciana* always exhibits the characteristic, markedly elongate postical decurrence diagnostic of the species.

In *P. miradorensis* the degree of decurrence postically is perhaps very slightly less extensive, rarely extending down for as much as 0.75 the merophyte length (Figs. 61:4; 62:7; 63:5). In the extremely slender-leaved forms with entire leaves (mod. *angustifolia-integrifolia*) the postical base is much less developed, and considerably less decurrent. The decurrence here ranges usually from 0.4-0.5 the merophyte length, only exceptionally to 0.6 this distance (Fig. 69:3, 5). The plants of this extreme also bear relatively short-decurrent antical leaf-bases (Fig. 69:4), and are probably genotypically distinct from *P. miradorensis,* s. str.; they are here described as var. *convoluta.*

Variation in leaf-shape.—The leaf of *P. ludoviciana* varies from obliquely and broadly ovate-triangular (type; Fig. 63:2), with the maximal length 1.3-1.5 × the leaf-width, to narrowly ovate-rectangulate. In the latter case, the leaf may be only very slightly ampliate (Fig. 66:13), with the length equal to 1.75-2.25 × the maximal width; such extremes are relatively rare, however. The minor variations of the preceding type of leaf-form share in common a nearly straight antical leaf-margin. The postical margin, by contrast, is usually at an 85-95° angle with the stem. *P. ludoviciana,* therefore, can be characterized as possessing a limited range of variability as regards the leaf shape. By contrast, in *P. miradorensis* we find an extraordinary diversity in leaf-shape. The leaves range from lanceolate-falcate to ovate-falcate or oblong-falcate to (rarely, and perhaps abnormally) shortly oblong. In the case of the "normal" ovate-falcate type, the antical leaf-margin is visibly arcuate (Figs. 68:6; 62:7), and the postical leaf-margin may be at an angle of 95-110° with the stem. In these cases, the length of the leaf usually ranges between the extremes previously given: *i.e.,* from 1.5-1.75 × the maximal width.

In more extreme cases, the leaf of *P. miradorensis* becomes 2.0-2.35 × as long as wide, obliquely lanceolate-falcate, with the distal portion

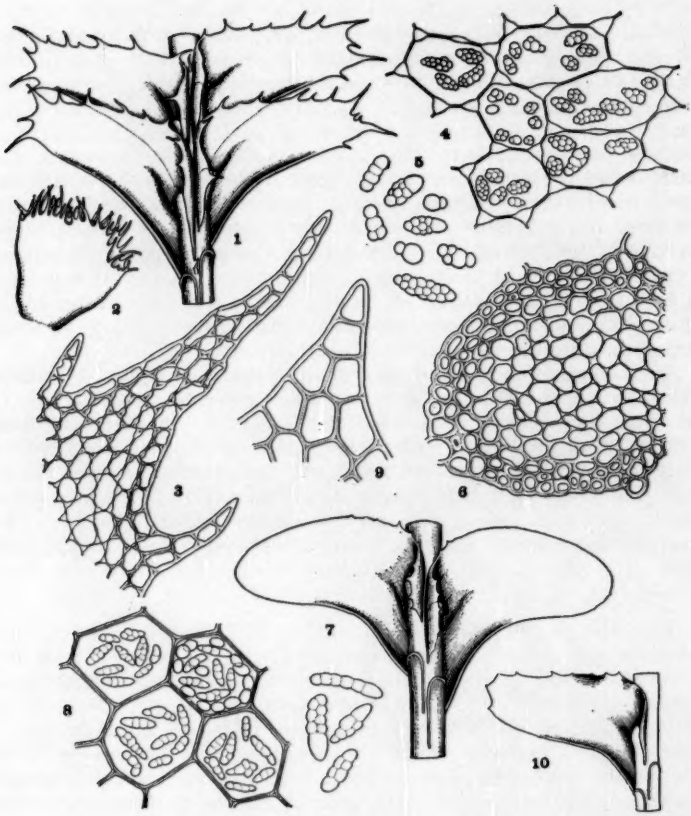

Fig. 62.—Sectios Hypnoides and Crispatae. 1-3, 8-10. *P. ludoviciana* Sulliv. (in 1-3, mod. *spinosissima;* in 8-10, mod. *integrifolia-viridis-leptoderma,* the *"P. tunarum"* extreme). 1. Shoot-sector, postical aspect (x 25); 2. Juvenile perianth, lateral aspect (x 16.5); 3. Leaf-apex, the middle tooth one of the large apical teeth (x 177); 8. Median cells with oil-bodies (x 560), at right individual oil-bodies (x 950); 9. Marginal tooth near leaf apex (x 345); 10. Leaf, *in situ,* postical aspect (x 14.5). 4-5. *P. hypnoides* Lindenb. 4. Median cells with oil-bodies (x 485); 5. Individual oil-bodies (x 865). 6-7. *P. miradorensis* Gottsche. 6. Stem cross-section (x 150); 7. Shoot-sector, postical aspect (x 16.5). (Figs. 1-3, *Schuster* 22987, Van Cleave, Miss. [see also Fig. 66:17-20]; 4-5, *Schuster* 26018, Highlands Hammock, Fla.; 6-7, *Whitehouse* 23318, Texas [see also Fig. 68:10-15]; 8-10, *Schuster* 26125, Collier-Seminole State Park, Fla.)

of the leaf prominently drawn out (Fig. 67:6-7, 14, 16). This extreme has been found occurring on the same plant (indeed, on the same shoot!) with the opposing extreme (Fig. 67:11, 12,18), in which the leaf is short-rectangulate and very wide, broadly rounded distally, strongly undulate, and only 1.3-1.4 × as long as wide. The shoots (or shoot-sectors) with this form of leaf closely simulate those of *P. undata* in many respects, and may be confused with them.

In general, however, *P. ludoviciana* has a more ovate-triangular leaf, with a nearly straight antical margin, while *P. miradorensis* has a narrower leaf, with a curved antical margin, the leaf being more drawn out, and clearly somewhat falcate. Usually the two species are separable at sight, on this basis. However, extreme forms of *P. ludoviciana* occur (Fig. 65), here tentatively separated as the var. *invisus*, in which we find a more attenuated leaf, *ca.* 1.85-2.0 × as long as wide, with a somewhat more falcate form than is "normal" in *P. ludoviciana*. The leaves in this case are also unusually strongly ampliate above the postical base (Fig. 65:6-8), and tend to have a strongly undulate crista, occasionally reflexed to a greater than normal degree (Fig. 65:1). Such plants serve to break down some of the value of a distinction between *P. ludoviciana* and *P. miradorensis*.

The sum total range within each of these two species thus goes from a leaf length of 1.3-2.25 × that of the leaf width, *on mature leaves*. On immature leaves, the width is proportionately greater. However, the variation in measurements given here cannot be regarded as due to allometric growth, since they are derived largely from plants of similar size (compare Fig. 66:5 and 13).

Variation in dentition of the leaves.—Typically, in *P. ludoviciana* the leaf-margins bear only 10-15 marginal teeth (7-13 *fide* Frye and Clark, p. 455, but this figure is certainly too low), as is the case in Sullivant's type material; these teeth are furthermore relatively small (4-6 cells long usually), except the two lobe-like apical teeth that are usually distinct, and which may be much larger.

In extreme forms, in which the plants are not at all luxuriant (female plants *ca.* 2.1-2.3 mm wide), an extreme development of marginal teeth of the leaves may occur, the longest, spinose ones being 10-12 cells long x 3-4 cells wide at base (Figs. 66:17; 62:1, 3); the teeth may be fewer, though, than in the other types, averaging 9-12 or 12-17 per leaf (as in *Schuster* 22987, Van Cleave, Miss.).

At the opposite extreme from these last two types is a form with the leaves entire or virtually so. The plants, though robust (*ca.* 3.5-3.8 mm wide) and with long-decurrent postical bases (which are distinctly cristate), show 0-3 (5-6) small teeth on the distal portions of the leaves, 0-5 on the postical margins and none on the postical, cristate bases (Fig. 68:22).

Careful field study suggests that in *P. ludoviciana* the notably coarse and strongly spinose teeth which are usually developed tend to be reduced, or even almost eliminated, when 1) the plants grow in excessive shade, and 2) they grow under unusually humid conditions. In such cases, the leaves retain a juvenile facies. (Immature leaves in this species are commonly quite edentate). Inversely, in at least some cases we find that plants growing under relatively xeric condi-

tions, in more direct light, tend to have strongly spinose dentate leaves (Fig. 62:1, 3). However, this is far from universally the case.

Preliminary study suggests that there are two such genetically controlled patterns of variation in the *P. ludoviciana-miradorensis* complex, each subject to some environmental modification. In the type plants (Fig. 63:2-3), and almost all other material seen of true *P. ludoviciana* (Figs. 64-66), the postical leaf-base, and the margin for some distance above the base, tend to be essen-

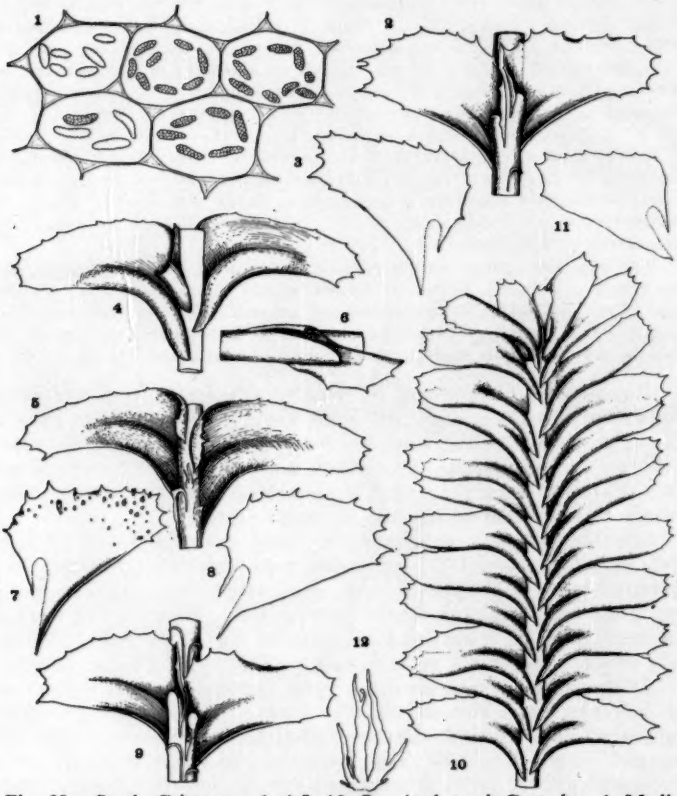

Fig. 63.—Sectio Crispatae. 1, 4-5, 10. *P. miradorensis* Gottsche. 1. Median cells with oil-bodies (x 550); 4-5. Antical and postical aspects of shoot-sectors, in 5 with minimal decurrence (x 12.5); 10. Sector of plant, antical aspect (x 12.5); 2-3, 6-9, 11-12, *P. ludoviciana* Sulliv. 2. Shoot-sector, postical aspect (x 12); 3, 7-8, 11. Leaves (x 13); 6. Lateral aspect of shoot-sector, with distal parts of leaf removed, showing insertion (x 13); 9. Shoot-sector, postical aspect (x 13); 12. Large underleaf (x 17). (Figs. 1, 4-5, *Schuster* 19184, n. of Escatawpa, Miss.; 10. *Schuster* 22110a, near Brooksville, Fla.; 2-3, 6-9, 11-12, from type of *P. ludoviciana* [see also Fig. 66:1-4].)

tially edentate, *while the teeth are developed with increasing robustness towards the leaf apex*. Inversely, in shade or weak forms of this type, the teeth are retained, or tend to be retained, at the leaf-apex, those in the basal half of the leaf being "lost" first. In the second type of plant, referred here to *P. miradorensis* (Figs. 68, 69), the *degree* of development of the teeth is reversed; the postical decurrent area retaining sharp, spinose teeth at nearly all times, while the distal portions of the leaves are edentate or virtually so (Figs. 62:7, 68:16), or may bear relatively low, scarcely spinose teeth (Fig. 68:1). Only in extreme cases do the plants of the *P. miradorensis* type lose the cilia or teeth of the postical leaf-base.

Of considerable interest is the fact that these two differing modes of dentition are correlated with the following character:

Variation in form of the crista or water-sac.—In the type plants of *P. ludoviciana* (Fig. 63:2, 9), and most other collections studied referable to this (Figs. 64-66), the decurrent postical "strip" is narrow and nearly or quite edentate; it is, furthermore, erect or squarrose rather than convolute. Consequently, in these plants there is formation of a crista (Figs. 61:7, 63:2, 9), or in the aggregate, an erect line of crests on the postical face of the stem (Fig. 64:6). Such a modification occurs to a lesser degree in the related *P. hypnoides*. In a minority of the regional plants examined, referred to *P. miradorensis*, the decurrent base is sharply reflexed or even distinctly convolute, forming a distinct "pocket" or water-sac in extreme cases (Figs. 61:4, 62:7, 67:16, 18). In such cases there is always correlated a development of 1-several sharply spinose teeth (on at least some leaves) of this basal, convolute region.

It has been customary in the literature (*e.g.*, see Herzog, 1932; Carl, 1931; Gottsche, 1863) to regard the plants developing only a "crista" as distinct specifically from those with a basal "pocket." The association of a different pattern of distribution of the marginal teeth (see above) suggests that these workers are correct in such an evaluation. However, study of a series of specimens shows that intermediate forms occur, which are clearly derived from *P. ludoviciana*. For instance, in *Schuster* 22975 (Fig. 64) the decurrent strip is usually edentate, but occasionally bears a single tooth; the crista here is narrowly reflexed. In *Schuster* 22987 (Fig. 66:17), the postical base may bear (0)-1-3 sharp teeth, on the most robust leaves (usually on fertile plants); in such cases it is distinctly, if not broadly reflexed, foreshadowing the "pocket" developed in true *P. miradorensis*. The occurrence of such leaves at first glance would almost invalidate any attempt to separate the present complex on the basis of the "presence" *vs.* "absence" of a postical "water-sac." In the less robust shoots of this collection (*e.g., Schuster* 22987) the postical base is in the form of a crista, and the crista is edentate or rarely bears a single sharp tooth. In such cases the resemblance to the uniformly cristate leaves of *Schuster* 22975 becomes remarkable. The similarity of these two plants in other respects is also remarkable: for instance, compare the densely ciliate perianth-mouth (Figs. 62:2; 64:7); the thick-walled, narrowly rectangulate cells of the postical leaf-base (Figs. 64:9, 66:18); the similar cells of the leaf-apices, with the marginal and apical cells tending to be rectangulate and somewhat elongated (Figs. 64:11; 66:20). The conclusion is inescapable that the plants of these two collections are very similar genetically, if not virtually identical.

A careful study of such plants, with some leaves bearing 1-2-3 teeth of the

postical bases, shows that, in spite of this deviant feature, they belong to *P. ludoviciana.* They resemble the latter (and differ from *P. miradorensis*) in several respects: (1) the leaves are sharply spinose-dentate in the distal half; (2) the postical decurrent base, dentate or edentate, is formed of prominently elongated, rectangulate cells with their longitudinal walls strongly thick-walled (due in part to confluence of the trigones); (3) the leaves are more ovate-triangular, with a nearly straight antical margin, on flattened leaves; (4) the ± elongate cells of the leaf-apices have the longitudinal (tangential) walls of the marginal several cell-rows ± thick-walled.

The considered conclusion of the author, then, is that the form of the postical leaf-base warrants a separation of what has, in our area, passed as *P. ludoviciana* into two distinct species.

Variation in cell form and size.—*P. ludoviciana* usually occurs as the mod. *pachyderma,* with the cells bearing bulging trigones (and, in the basal median cells, scattered intermediate thickenings on the longer walls). The cells of the apex, and on the margins, tend to become somewhat, but never prominently, elongated parallel to the leaf-margin; they furthermore are often ± thick-walled, parallel to the margins with the consequence that the trigones become nearly obliterated. The secondary thickening is developed largely on the walls parallel to the leaf-margins. This is particularly prominently the case, in many phases, in the area near the postical, decurrent portion of the leaf (Fig. 66:10, 18); the cells in such cases may be perfectly rectangular and average 10-12 (13) x (35) 40-50 μ in length. In less extremely xeromorphic phases, the cells of the postical base appear less elongated (Fig. 66:2, 6), and show confluence of the trigones to a lesser extent.

The previous manifestations (see Figs. 64; 66) show how polymorphic the pattern of wall-thickening may be in this complex, even in "normal," pachydermous phases. In all these cases, the median cells, and those at median base, are clearly provided with coarsely bulging trigones. In the extreme shade forms of *P. ludoviciana,* the trigones may be much reduced everywhere in the leaf. In the most extreme case seen, the walls are very slightly equally thick-walled, without trace of trigones. In all these various types, the basic dimensions of the cells remain essentially unchanged, although the proportions of the cells near the postical leaf-base are quite radically different in *P. ludoviciana* and *P. miradorensis.* In the most extreme phases, the mod. *integrifolia-leptoderma,* the cells of the postical base are only slightly differentiated, averaging only 1.5-2.5 × as long as wide (Fig. 65:11-12). In such cases, the walls are not or little thickened (and the longitudinal walls are not differentiated from the shorter cross-walls). Such cases are relatively rare, and it seems warranted to consider the tendency for formation of a basal area of narrow, rectangulate cells as a "normal" manifestation in *P. ludoviciana,* hence of systematic importance. The form of these cells of the postical base emerges most clearly when they are compared to those of the median base of the leaf (cf. Figs. 64:9, 10; 65:12, 13; 66:10, 11; 66:18, 19; 67:3, 4).

In contrast to this differentiation of a postical region of elongated cells stands the simpler condition in *P. miradorensis.* In this species the cells of the postical flap are collenchymatous exactly like the median basal cells — *i.e.* bear nodose trigones, which are sharply defined

and not confluent. Consequently, the basal cells never develop equal, strong, longitudinal walls. Furthermore, the basal cells are more nearly isodiametric (Figs. 67:10; 68:3, 7, 12, 18). In the forms with a relatively narrow, edentate postical flap (var. *convoluta*), the cells may be slightly elongated, and twice as long as wide.

Variation in propagula formation.—Normal manifestations of *P. ludoviciana* and *P. miradorensis* are always abundantly propaguliferous. However, under extremely shaded conditions (as in the deepest, permanently shaded portions of hammock forests, with a light intensity never exceeding 12 foot candles) and under unusually moist conditions (as along streams), *P. ludoviciana* may be habitually without propagula. Furthermore, such extreme shade (and/or high moisture) forms also show a high level of reduction of the dentition. On these two bases, such forms may be confused with *P. undata.* However, all such phases of *P. ludoviciana* seen show formation merely of a crista —never of the reflexed, convolute basal region characteristic of *P. undata.* Leptodermous, propagula-free phases of *P. miradorensis* have not been seen.

It should be emphasized at this point that the immediate relatives of *P. ludoviciana* found in the wet montane rain forests of the Cordilleras of South America, and in the dense tropical rain forests of that continent, normally fail to exhibit any trace of propagula. It is hypothesized that either the plants must occur in exposed areas with at least intermittently high saturation deficit, or in areas with a good deal of insolation, or both, before propagulum development is initiated.

Variation in form of the female bracts.—The female bracts of the *P. ludoviciana* complex undergo almost as wide a series of variations as do the vegetative leaves. Furthermore, the variation is usually clearly parallel to that of the leaves. This is clear when we compare the leaves (Fig. 66:5) with the bracts (Fig. 61:1, 3) of one of the less extremely dentate forms, in which the postical leaf-base is always entire (*Schuster A*-109). The leaves here bear *ca.* 9-18 rather moderate-sized or small teeth, and the leaf averages *ca.* 1.5-1.6 × as long as broad. The bracts in this case average *ca.* 1.5 × as long as broad, and bear rather moderate-sized teeth, 24-28 per bract. If a sharply spinose-dentate phase is studied (Figs. 62:1, 3; 64:1; *Schuster* 22975, 22987) the leaves are seen to bear 10-18 longer, more jagged teeth; the leaves average 1.6-1.9 × as long as broad. In such cases the corresponding bracts average 1.6-1.9 × as long as broad, bear sharper, more uneven, jagged teeth (often more numerous, ranging to 36-45 per leaf; see Fig. 64:2-3).

On the other hand, phases with subentire leaves (var. *invisus;* Fig. 65:1, 2) may have the bracts coarsely dentate. In the illustrated case, note that the ampliate postical base is particularly coarsely dentate, although the teeth are unusual in their irregular form and disposition, and in being scarcely sharp at the summit. The two bracts (Fig. 65:9-10) shown also illustrate the great variability in development of teeth of the antical leaf-margin.

The antical, convolute margin of the bracts may bear only 2-3 teeth near its apex (Fig. 64:3); in other cases the teeth may extend down to the basal third of the bract, and number 4-6 along the antical margin (Fig. 65:9). Study of the excellent figures given by Gottsche (1863) of the female bracts of the various species he described (here listed in synonymy under *P. ludoviciana*) indicates an even more extensive range of variation. In particular, some of the plants figured by Gottsche possess female bracts whose antical margin is spinose-dentate to the base. This only rarely occurs in our plants of *P. ludoviciana*, and then the antical teeth are small.

In *P. miradorensis* the bracts, like the leaves, tend to be more strongly attenuate. The bracts vary from 2400-2700 μ long x 1050-1350 μ wide, gradually tapering to a width of only 350-450 μ before the somewhat truncated apex. The antical margin is strongly convolute, and may bear obscure low teeth to within the basal third of the margin. The postical base (which tends to be convolute) and margin bear spinose teeth, which become progressively less sharp and marked towards the 3-4-dentate apical portion of the leaf. The postical base, on the antical margin, may bear isolated lamellate teeth (Fig. 70:1,3).

Study of a series of female bracts thus appears to demonstrate that (a) their dentition, in both species, tends to be coarser and more ample than that of vegetative leaves; (b) *P. ludoviciana*, even in attenuate-leaved extremes like the var. *invisus*, has relatively short female bracts, never twice as long as wide; (c) *P. miradorensis* has the female bracts strongly drawn out, like the leaves, and fully twice as long as wide. This difference in shape of the bracts is probably of systematic value.

Variation in form and dentition of the perianth.—Although neither androecia nor gynoecia of *P. ludoviciana* have been described, gynoecia are frequently produced. The writer, however, has seen only a few androecial plants. Gottsche (1863) has described the perianths of several of the Mexican "species" here regarded as identical with *P. ludoviciana*. Although gynoecia are rather frequently developed, fertilized archegonia have never been seen. Associated with this, it is customary to find only rudiments of the perianth.

Archegonial plants of both *P. ludoviciana* and *P. miradorensis* (cf. *Schuster* 22085a), at time of maturation of the archegonia, do not show any trace of a recognizable perianth. The archegonia are surrounded by a pair of presumably perichaetial bracts, completely free at the base, which are less than one-half the length of the leaves, but strongly ciliate from their middle upward (Fig. 61:5). These bracts are only *ca.* 600 μ long, broadly suborbicular to obovate and are strongly ventricose and closely approximated (with the archegonia thus in a chamber formed by them, and completely hidden from view). The archegonia number *ca.* 12 (with several rudimentary ones); at time of their maturation there is no trace of a true perianth at their base. In almost every case seen, correlated with the cessation of growth of the shoot subsequent to initiation of archegonia, a single lateral innovation developed below the archegonial group (in the axil between the putative perichaetial bract and the normal vegetative leaf below it).

With study of further collections (*Schuster* 22975), it becomes evident that

the putative perichaetial bracts of the previous collection (*Schuster* 22085a) are really equivalent to the undeveloped, deeply bilabiate, perianth. In the material of *Schuster* 22975, plants with postmature archegonia, surrounded by a pair of short, broadly obovate bracts are rather common. In this case, however, the broad and short ciliate bracts are "fused" postically to a slight extent (0.2-0.4 their length) but fused nearly their entire length dorsally, thus constituting a real perianth. Their distal, free margins are closely ciliate much as are the margins of the free bracts. It is thus evident that, without fertilization, a perianth may or may not be formed in this species — depending on whether the two bracts homologous with the perianth are connate dorsally and ventrally or not. When connate, the point of union dorsally is sharp, and may be very narrowly winged, while the shorter line of fusion ventrally is not perceptibly winged. In *Schuster* 22975, as in the previous collection, the development of archegonia results in most (but not all) cases in the development of an innovation directly below the perianth. A plant where such innovation does not take place is shown in Fig. 64:1. It is of some interest to note that fertile archegonial plants may be freely propaguliferous (as in *Schuster* 22975), leaves immediately below the perichaetial bracts bearing propagula.

In only a few cases have I been able to find what may be considered mature perianths. These, however, may be produced without fertilization having taken place. Since the species, in our area, consists almost wholly of populations of the female sex (or else includes male populations unable to produce androecia), it seems improbable that mature perianths are frequently produced.

However, in a series of collections, all uniformly female, the mature perianth appears to be developed — without previous fertilization having taken place (the archegonia being largely disintegrated). The formation of perianths here did not appear to result in any inhibition of propagula formation — even the perichaetial bracts showing propagula, on both upper and lower leaf-surfaces.

In these exceptional cases, where mature perianths were developed, the perianth mouth is rather shortly ciliate-dentate, with the teeth quite similar to those of the leaves and bracts; the teeth are furthermore, relatively remote from each other (Fig. 61:1, 2). In the several instances where immature perianths were found, the perianths were generally closely ciliate, with slender, uniseriate cilia (Figs. 64:7, 8; 62:2). This range of variation in degree of development of the cilia appears impressive at first. It must be kept in mind, however, that this is correlated to some degree with differences in degree of dentition of the leaves. Plants with sharply spinose-dentate to spinose-ciliate leaf-margins have the perianth-mouth ciliate to ciliate-laciniate. Inversely, plants with rather finely dentate leaves appear to have the perianth mouth relatively finely and distantly dentate or spinose-dentate. This correlation is far from uniform. In the attenuate-leaved var. *invisus* (Fig. 65) the leaves are almost entire-margined, but the immature perianths seen were densely and strongly ciliate-laciniate (Fig. 65:3-4). Preliminary studies thus suggest that the differences in dentition of the perianth-mouth are of minor systematic significance, but, admittedly, study of longer series of female plants may show cor-

relation of differences in this feature with other more significant characters.

The form of the perianth also appears somewhat variable. The mature perianths seen were clearly asymmetrical, in lateral view, with the antical keel about twice the length of the postical (Fig. 61:1, 2). In these cases, the area adjacent to the postical keel was compressed, that adjacent to the antical keel, inflated (except at the mouth). The juvenile perianths show, in some cases, a similarly abbreviated postical keel (Fig. 64:7), but in other cases the postical keel is only slightly shorter than the antical. A similar variation characterizes the Mexican plants illustrated (under a variety of species names) by Gottsche, although the perianth mouth in these is rarely as extremely obliquely terminated as in Fig. 61:2.

In almost all cases seen, the antical keel of the perianth, which never appears to run up to the summit of the perianth, is very narrowly winged, and the wing gradually disappears above. Only in *P. ludoviciana* var. *invisus* does the antical keel ever suddenly end in a distinct tooth (Fig. 65:3).

P. miradorensis appears to be extremely similar to *P. ludoviciana* in regard to the perianth. The mature perianth is essentially identical to that of *P. ludoviciana*, with the antical keel longer than the postical, and with the compressed lower portion of the mouth tending to be reflexed. Gottsche (*loc. cit.*) has figured the perianth of the type of *P. miradorensis* as having a well-developed antical keel, bearing several teeth. The mature perianths seen (*Schuster* 19250b) agree in this respect with Gottsche's type, and with the few other Floridian collections seen bearing immature perianths. The little perianth-bearing material seen of *P. miradorensis* shows a narrower range in dentition of the mouth than that so far found in *P. ludoviciana*.

The highly similar perianths of *P. ludoviciana* and *P. miradorensis* thus show only one difference of any systematic value: the antical keel of the perianth of the former species tends to be short and edentate, at most ending in an obtuse tooth, while in *P. miradorensis*, the longer antical keel bears 2-4 teeth; the latter may be low and inconspicuous.

Variation in the degree of development of the underleaves.—The *P. ludoviciana-miradorensis* complex always possesses at least vestigial underleaves. These appear to have been overlooked in a few of the plants described (as separate species) by Gottsche, from Mexico; *e.g.*, in *P. schliemiana* var. *b*. The degree of development of the underleaves is subject to a very great degree of variation, as was noted as long ago as 1896 by Evans. In some populations they consist of a few cilia, free almost to base (Fig. 69:6-7), in other cases, of a small lamellate base, divided distally into several long cilia (Fig. 67:15) in still other cases they are larger, and divided almost to base into 2-several acuminate, tortuous laciniae and/or cilia (Figs. 65:5; 68:22).

An analysis of the variation-pattern in the underleaves allows a distinction of two fundamental types: (a) underleaves consisting basically of 2-several long tortuous cilia, which are uniseriate for their whole length, or perhaps 2-3 cells wide at base; (b) underleaves consisting of usually 2 linear-lanceolate laciniae, ending in a uniseriate row of cells, but 4-8 cells wide for much or most of their length, and

clearly united basally into a broad if short lamella; in addition to the 2 linear-lanceolate segments, secondary, shorter and narrower cilia or laciniae are normally produced. The first type of underleaf is correlated with the attenuate-leaved plants bearing a basal "pocket," *i.e.*, with *P. miradorensis*-like plants. The second type is always characteristic of plants with merely cristate bases, *i.e.*, with *P. ludoviciana*-like plants.

This distinction into two modes of variation breaks down in the exceptional cases where *P. ludoviciana* has rudimentary underleaves. These then may consist of short laciniae that are so narrow as to approach the cilia of *P. miradorensis* (Fig. 66:17).

There is no necessary correlation between robustness and degree of development of the underleaves. In some of the weaker forms, with obscurely dentate leaves, of shaded damp sites (*P. ludoviciana* var. *invisus*) the underleaves may be extremely large and well-developed (Fig. 65:5-7). Inversely, robust plants may have the underleaves so reduced that they are almost impossible to demonstrate (Fig. 61:7).

This absence of any obvious correlation between size of the plant and underleaf size is particularly well-marked in the tropical plants, from South America, which are either conspecific with *P. ludoviciana*, or else so closely allied as to be hardly separable, *e.g.*, *P. guilleminiana*, *P. oreocharis* and *P. rhizophila*. These taxa are discussed under *P. ludoviciana* (pp. 89-94). In them we may find robust plants, 4-5 mm wide and to 4-6 cm long or more, in which the underleaves are almost vestigial. The longly decurrent postical bases of the leaves are here closely juxtaposed, hence the ventral merophytes have been perceptibly narrowed. It is still questionable to what extent the relative reduction of the ventral merophytes is a valid criterion in the distinction of species. I have, tentatively, considered such variation intraspecific, especially since it does not appear linked with other diagnostic features. This matter, however, needs much more, and careful, future investigation.

The preceding analysis and accompanying illustrations have shown that the *P. ludoviciana-miradorensis* complex (as represented in our area) shows a bewildering degree of variability. Some of the extreme variations can probably be largely or entirely attributed to environmental stimuli; others appear to be genetically determined (with a limited amount of environmentally-induced variation superimposed). At present it is almost impossible to separate these two sources of variability. As a consequence, the recognition of varieties within the species (and/or recognition or segregation of additional species from the complex) appears unwarranted, with few exceptions. The following summary, in key form; analyzes some of the most significant variations which the writer has found in our material. For the presumably environmentally-induced variation the terminology of Buch (*i.e.*, the term "modificatio") is used. *P. undata* is not included in this key since its strongly crispate leaves serve to separate it from the other taxa treated here. In the key *P. hypnoides* is included, owing to the fact that it has been universally confused, in the North American literature and herbaria, with the *P. ludoviciana-miradorensis* complex.

KEY TO SPECIES AND VARIATIONS IN SECTIO HYPNOIDES AND SECTIO CRISPATAE

1. Leaves with postical base prominently long-decurrent on mature shoots, the decurrent strip running down for (0.45) 0.55-0.85 the merophyte length, and for *ca.* (0.45) 0.55-0.75 the length of the decurrence antically. 2
   2. Postical base erect, not reflexed or convolute, edentate (rarely with 1-2 teeth), forming a crista, relatively narrow; leaves with dentition tending to be reduced in basal half of leaf: the decurrent base without discrete spinose teeth, the apex almost always ± dentate or spinose-dentate; underleaves normally formed of 2-several laciniform, tortuous lobes (each 3-several cells broad at base). Cells of decurrent postical strip ± rectangulate, (1.5) 2-5 × as long as wide; cells in leaf-apex (near margins) tending to be elongated parallel to margin. ***P. ludoviciana*** Sulliv. 3
      3. Leaves ± sharply spinose-dentate, at apex usually with 2-3 (> 5) very coarse apical teeth, the postical margin usually with 5-10 less coarse teeth; cells ± strongly collenchymatous; propagula freely produced; underleaves small to large: their length rarely approaching the leaf-width. 4
         4. Leaves relatively broad: averaging 1.35-1.55 × as long as wide; postical, decurrent strip and area immediately above it, formed of ± collenchymatous cells averaging 1.5-3 (4) × as long as wide; perianth-mouth rather shortly, irregularly laciniate-dentate; teeth of leaves relatively coarse and short, obtuse to acute, broad-based. (Mesic phase?) Typical phase .....(Mod. *latifolia-dentata*).
         4. Leaves slender and elongate: averaging (1.65) 1.72-2.0 (2.2) × as long as wide; postical decurrent strip and area above it of prominently thick-walled cells (the longitudinal walls often undulate), averaging 3-5 × as long as wide; perianth mouth densely, longly ciliate with predominantly uniseriate cilia; teeth of leaves slender, acute to spinose, 1-2 (3) cells wide x 3-8 cells long, or longer. 5
            5. Leaves with the dentition confined strictly to distal ¾ of the leaf, the postical base uniformly edentate; postical base never reflexed to any degree; teeth of distal half of leaf moderately spinose, 1-2 (3) cells wide x 3-8 cells long usually. ....Mod. *angustifolia-dentata*
            5. Leaves (or some of them) with dentition extending down to the decurrent postical base, the base then with 1-2 (3) small but spinose teeth; postical base often somewhat reflexed, but never convolute; teeth of distal half of leaf strongly spinose, 2-5 cells wide x 8-12 cells long. .....Mod. *angustifolia-spinosissima.*
      3. Leaves entire to subentire, the apex commonly with 2-3 low, obtuse remnants of teeth, the postical margin entire or rarely with isolated low teeth; cells never with strongly bulging trigones, the walls ± thickened; propagula absent; postical decurrent strip of little elongate cells (1.5-2.5:1), their walls not prominently thickened. 6
         6. Leaves broad: averaging 1.35-1.6 × as long as wide on mature shoots; plants shiny in texture; underleaves vestigial, less than 0.3 the leaf-width in length. .....Mod. *leptoderma-latifolia-integrifolia.*
         6. Leaves slender, somewhat falcate: averaging 1.85-2.1 × as long as wide; plants dull; underleaves large, often 0.7-1.0 the leaf-width

in length. .....
.....var. *invisus* var. n. = Mod. *leptoderma-angustifolia-integrifolia.*

2. Postical base distinctly dilated, broadly reflexed, the reflexed margin ± distinctly involute (the base thus ± tubular), the margin of the thus-formed pocket usually with (0) 1-6 sharp cilia or teeth; leaves with distal halves bearing small. low regular teeth (sometimes reduced to 1-several very small or obscure teeth; in many cases absent, or reduced to 1-2 apical teeth); underleaves normally formed of 2-several uniseriate, tortuous, long (sometimes branched) cilia, which are free virtually to base; cells of decurrent, reflexed leaf-base isodiametric or little elongated (length 1-1.8:1 usually), the cells collenchymatous like other leaf-cells; cells in leaf-middle, and in apex, as well as marginal cells almost uniformly isodiametric, the marginal collenchymatous like inner cells (never forming a thick-walled border). *P. miradorensis* Gottsche. 7

7. Postical leaf-bases relatively broadly reflexed-convolute, the border of the reflexed region usually 2-6-ciliate or dentate; leaves long-decurrent postically and antically: postical decurrence ranging from 0.55-0.75 the merophyte length; leaves usually ± dentate in distal halves. (*P. miradorensis*, typical). 8

8. Leaves regularly dentate, the teeth low but discrete, usually 8-16 above the postical reflexed base; leaves very narrow and falcate: 2.0-2.35 × as long as wide. .....Mod. *angustifolia-dentata.*

8. Leaves with apex rounded, truncate-bidentate, or ending in a single tooth, occasionally with a few obscure teeth elsewhere on postical margin; leaves broader, less than 1.85 × as long as wide. .....Mod. *latifolia-integrifolia.*

7. Postical leaf-bases narrowly reflexed-convolute, the reflexed border 0-1 dentate usually; leaves short-decurrent antically and postically: the postical decurrence ranging from 0.4-0.55 the merophyte length usually; leaves very narrow, 2.0-2.2 × as long as wide, entire-margined (except for 1-3 small apical teeth). .....
.....*P. miradorensis* var. *convoluta* (Mod. *angustifolia-integrifolia*).

1. Leaves with postical base short-decurrent on mature shoots, the decurrent strip running down for 0.2-0.35 the merophyte length, and only for 0.2-0.35 the length of decurrence of the antical portion of the leaf; postical leaf-base dilated, erect or nearly so, forming usually a distinct crista, never reflexed-convolute; leaf-margins always sharply and rather regularly spinose-dentate, the teeth (on mature leaves) extending down virtually to the postical base; underleaves lamellate, sometimes lobed, the margins bearing usually short cilia or teeth, rarely divided into several laciniae. .....
.....*P. hypnoides* Lindenb.

PLAGIOCHILA LUDOVICIANA Sulliv.

Figs. 61:1-3, 7-8; 62:1-3, 8-10; 63:2-3, 7-9, 11-12; 64-66; 67:1-5; 68:22-25

? *Plagiochila guilleminiana* Montagne, *in* Lindenberg, Spec. Hep., 152, 1844; Herzog, Svensk Bot. Tidskr. 46(1):70, figs. 5-9, 11d, 12a-b, 1952.

? *Plagiochila rhizophila* Spruce, Trans. and Proc. Bot. Soc. Edinburgh 15:495, 1884-85; Herzog, Svensk Bot. Tidskr. 46(1):72, fig. 74-f, 1952.

? *Plagiochila oreocharis* Spruce, Trans. and Proc. Bot. Soc. Edinburgh 15:498, 1884-85; Herzog, Svensk Bot. Tidskr. 46(1):72, fig. 7a-d, 1952.
Plagiochila ludoviciana Sulliv., Musci Alleg. (Exsic.) No. 223, 1845; Sulliv. Amer. J. Sci. and Arts II, 1:73, 1846; Evans, Bot. Gaz. 21:192, pl. 16, figs. 4-12, 1896, in part.
Plagiochila patula var. *b leiboldii* Gottsche, Mex. Leverm. 105, pl. 2, 1863.
Plagiochila aliena Gottsche, Mex. Leverm. 118, pl. 1, 1863.
Plagiochila schliemiana Gottsche, Mex. Leverm. 123, pl. 1, 1863 (at least as to var. *b*).
Plagiochila schiedeana Gottsche, Mex. Leverm. 149, pl. 9, 1863.
Plagiochila subcristata Gottsche, Mex. Leverm. 150, pl. 10, 1863.
Plagiochila plicata Lindenb. et Gottsche, *in* Nees, Gottsche et Lindenb., Syn. Hep. 644, 1847?; Gottsche, Mex. Leverm. 152, pl. 9, 1863.
Plagiochila punctualis Gottsche, Mex. Leverm. 153, pl. 10, 1863.
Plagiochila tunarum Stephani, Spec. Hep. 2:189, 1906 (Cuba, *Wright*).
Plagiochila undulifolia Herzog, Hedwigia 72:219, fig. 11, a-f, 1932 ?

Plants robust, usually in loose patches or dense mats, dull to deep green to yellowish or olive-green, but never strongly brownish, dull, showing strong differentiation into a creeping rhizomatous stem-system and sharply ascending aerial leafy stems that stand away at an angle from the (usually vertical) substrate. *Mature aerial shoots* 2.5-4.2 (4.7) *mm wide,* infrequently furcate or *pseudodichotomous* (but frequently with 1 or often with 2 elongate innovations below the female inflorescences), rarely with solitary monopodial branches. Stems *ca.* 200-235 μ, occasionally 260-310 μ in diameter, the cortical cells strongly thick-walled, somewhat brownish, in 2-3 (4) layers, slightly smaller in diameter than the thin-walled medullary cells; medullary cells in at least 8 layers. Rhizoids on aerial shoots absent or virtually so. Leaves always *strongly imbricate, widely and nearly horizontally spreading* when moist *in a nearly flat plane,* at an angle of 75-85° (95°) with stem-apex; *postical margin usually at an angle of* 90-100° (rarely 110°) *with stem-apex; leaves narrowly obliquely ovate to ovate-falcate,* varying from 0.95-1 mm wide x 1.25-1.35 mm long to 0.97-1.1 mm wide x 1500 μ long (*type!*) to 750 μ wide x 1650 μ long to a maximum of 1500 μ wide x 2500 μ long (the *leaf-length ca.* (1.35) 1.45-1.7 $\times$ *as long as its subbasal width*); leaves with insertion exceedingly elongate (*the line of insertion ca.* 0.85-1.1 $\times$ the leaf-width), the dorsal base exceedingly long-decurrent; antical margin suberect basally (40-45° with stem), gradually arching outward and concave, the distal half of the antical margin eventually widely spreading ([75] 85-100° with stem), ventral (anterior) margin *strongly arched and dilated above the base, but virtually straight on distal two-thirds of leaf;* leaf apex usually narrowly truncate or rounded-truncate, sometimes subacute; *postical base long-decurrent* (*decurrent strip broad, standing stiffly away from the postical-stem surface to form a crista, but not strongly reflexed to form a postical pocket*), the decurrent portion wide, extending typically for 0.4-0.7 the merophyte length; *decurrent strip edentate;* postical margin above base usually with 5-10 more or less spinose marginal teeth; leaf-apex with generally 3-5 spin-

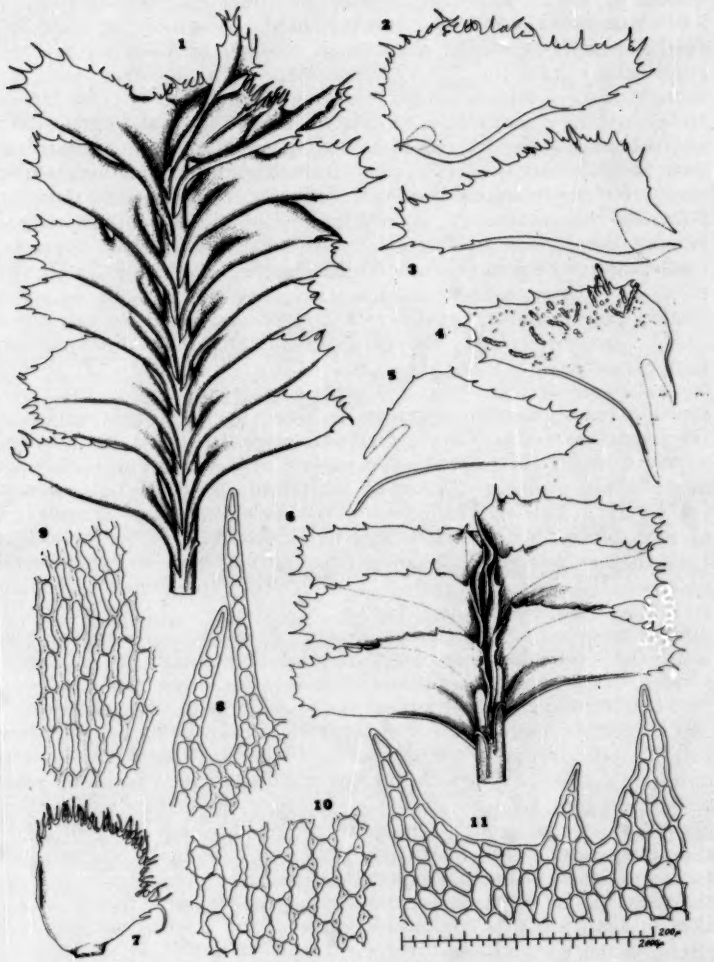

Fig. 64.—*Plagiochila ludoviciana* Sulliv. 1. Shoot with juvenile perianth, propagulum-free (x 16.5); 2-3. Female bracts (x 16.5); 4-5. Leaves (x 16.5); 6. Shoot-sector, postical aspect (x 16.5); 7. Juvenile perianth (x 16.5); 8. Cilia of perianth-mouth (x 182); 9. Cells of base, along decurrent strip (x 182); 10. Cells of leaf-base, along midline of leaf (x 182); 11. Cells of leaf-apex (x 182). (All from *Schuster* 22975, Van Cleave, Miss.; figs. 2-7 drawn to bottom portion of scale; figs. 8-11 drawn to top portion of scale.)

ose apical teeth; distal one-third of antical margin often with 1-3 spinose teeth (the marginal teeth of the entire leaf varying from *ca.* 9 to a maximum of 16 [*type*], rarely, in mod. *spinosissima* up to 22-26); cnemis strongly developed, the median leaf-base medially strongly longitudinally sulcate for 1/3-1/2 the leaf-length, together with the strongly reflexed antical margin resulting in an elongate, often falcate, arched convex dorsal fold extending for 0.4-0.6 the leaf-length. Apical and subapical cells (14) 16-18 x 18-23 μ to 20 x 20 μ; median leaf-cells 18-23 μ wide x 25-32 μ, the walls slightly or not thick-walled, except for the marginal 1-several cell-rows, *which usually have* $\pm$ *thickened tangential walls,* elsewhere the *trigones normally coarse and bulging,* occasionally confluent; cells at middle of leaf-base averaging 1.5-2 times as long as wide, from 20-21 x 30-40 (44) μ to 24-26 x 32-40 μ, with coarse, often $\pm$ confluent trigones. Cells of the decurrent postical base variable, usually *with longitudinal walls strongly thickened,* nearly evenly so, the cells becoming narrowly rectangulate (length-width 3-4:1) and then 12-13 (15) x (30) 36-43 (55) μ. Oil-bodies usually 4-9 per cell, *distinctly segmented,* varying from very coarsely, few-segmented (segments to 3.5 μ) to more finely segmented (segments *ca.* 1-2 μ), the individual segments always protuberant; segments usually in 1-3 rows (on superficial examination); oil-bodies mostly ovoid to linear-ellipsoid or baciliform, 3-4 x 6-7.5 μ, a few to 3-4 x 9-10 μ; chloroplasts 3.5-4.5 μ. Underleaves *always distinct,* but usually difficult to see, often largely hidden, varying from vestigial (and then of 2-several laciniae or cilia) to *plurilaciniate, occasionally of 2-several acuminate segments,* to 700-1000 μ long, usually with several weaker subbasal cilia. Asexual reproduction almost universally present (even on the perichaetial bracts), *by means of leafy propagula* from the postical (more rarely to some degree also antical) leaf-surface, the propagula deciduous with age; the *leaves persistent.*

Female inflorescence terminal, most often with one, occasionally two elongating innovations from beneath the lower half of the leaf-axil(s); perichaetial bracts similar to leaves, less decurrent, 1.6-1.85 mm long x 1100-1250 μ wide (or larger; measurement based on plant with leaves only 1.2-1.5 mm long), similar to leaves, but with postical margin relatively strongly undulate-crispate, bearing 22-26 or 32-40 sharply spinose, rather *irregularly sized teeth;* teeth largely confined to postical margin and apex of bracts, but 2-5 (occasionally 5-8) on the distal 0.5-0.7 of the convolute antical margin, more rarely the antical margin nearly as copiously dentate as the postical margin; base strongly concave and sheathing the terete basal portion of perianth. Perianth strongly laterally compressed above, but nearly terete near base with a long dorsal keel (length to mouth *ca.* 1.75-2 mm dorsally), but usually a very short postical keel (length *ca.* 0.4-0.5 the dorsal keel); *dorsal keel not or narrowly winged,* the wing entire; postical keel unwinged; mouth very wide, partly as a consequence of the $\pm$ oblique truncation, the width of the mouth often equal to or greater than length of dorsal keel; only dorsal portion of perianth inflated, but the broad postical portion strongly compressed down to perianth-

base, forming a broad flat "wing" that is often reflexed; perianth-mouth ± densely, strongly spinose-ciliate, the cilia uniseriate nearly to base, to 10-12 cells long, close; cells of cilia *ca.* 18 μ long x 13-15 μ wide.

Type.—Louisiana (*Sullivant,* Musci Alleghaniensis Exsic. No. 223, 1845). (Figs. 63:2-3, 6-9; 66:1-4.)

Distribution.—A very common and polymorphous neotropical species, whose range to our south is still very imperfectly understood, since presumed variants of it have been described as discrete species (particularly by Gottsche, Stephani and Herzog), from Mexico southward to Bolivia. The problem of the neotropical range of *P. ludoviciana* is difficult to solve, since the descriptions (and, if given, the illustrations) of closely allied taxa are often meaningless or nearly so.

Detailed, exhaustive studies of the variation of North American material of *P. ludoviciana* have demonstrated a very great polymorphism in this species. This polymorphism is partially the consequence of the varied environmental conditions the species occurs under, but is evidently also in part genetic in nature. It seems impossible to link the individual modes of variation (of the individual characters) into any pattern. Consequently, the species is broadly delimited here. The variability is discussed in detail, *vis-a-vis* that of *P. miradorensis* on pp. 71-85.

The excellent illustrations of Gottsche (1863) indicate that as many as six, possibly seven, taxa recognized for Mexico in this complex are inseparable from *P. ludoviciana.*

Under the name *P. plicata* Gottsche (1863) figures two forms (*a* and *b*). His fig. 7, of the form *a* suggests a long-decurrent postical leaf-base. In this case, the plant would fall in the *P. ludoviciana* complex. However, some of the other figures given (particularly of the var. *b*) suggest a short-decurrent form, similar to *P. hypnoides, P. serrata* and their relatives, to which Gottsche also compares them. Similarly Gottsche's *P. patula* var. *leiboldii* appears quite inseparable from forms of *P. ludoviciana.* However, it is very questionable whether it has anything to do with *P. patula* s. str. The latter was described from Jamaica (Swartz, Fl. Ind. Occ. III:1844, 1806); Lindenberg (Spec. Hep. Fasc. I:pl. 3) illustrates it as with a notable short-decurrent postical base. If this illustration is correct, *P. patula* is quite distinct from *P. ludoviciana* s. lat. In contrast, *P. patula* var. *leiboldii* has a leaf-form, dentition of the leaves, and long-decurrent cristate leaf-base closely matching many forms of *P. ludoviciana.*

Unfortunately, with the destruction of the Gottsche collections at Berlin, the synonymy cannot be determined at this date with any absolute certainty. Where possible doubt exists, the Gottsche species have been indicated in synonymy by a question mark.

Material from Panama has been seen (NYBG), sub "*P crispula* Lindb." (leg. W. Seeman), which appears inseparable from *P. ludoviciana.*

It is possible that *P. ludoviciana* Sulliv. is conspecific, although certainly not totally identical, with *P. guilleminiana* Mont., a very widespread neotropical species ranging from Ecuador to Bolivia, possibly to Brazil and Paraguay (see Herzog, 1952, p. 75) and to Nova Granada. Since reduction to synonymy of *P. ludoviciana* under the

earlier *P. guilleminiana* must involve comparison of the type plants, and since the type of the latter species is not available to me at present, it appears unwise to "sink" *P. ludoviciana* at present. Nevertheless, *P. ludoviciana* shares in common with *P. guilleminiana* a long and impressive series of suggestive features, among them: (1) leaves ovate-triangular, with both antical and postical bases long-decurrent (compare Herzog's [1952] Fig. 6a, of the type of *P. guilleminiana* with my Fig. 66:1, the type of *P. ludoviciana*); (2) the dentition of the leaves most marked distally, the area above the decurrent base, and the margin along the decurrent base, essentially or quite edentate; (3) perianth generally without a toothed antical keel, the antical keel either weakly carinate, or (at least on juvenile perianths) sometimes ecarinate (compare Herzog's Figs. 5f, 9c, with my Figs. 61:1-2; 64:1, 7); only rarely is the antical perianth keel well-marked and then may end abruptly in a blunt to acute tooth (compare Herzog's Fig. 8d with my Fig. 65: 3); (4) the female bracts are, in both instances, much more strongly ciliate-dentate to spinose-dentate, as compared with the ordinary vegetative leaves (compare Herzog's Figs. 5a and e, 8c, and 9b with my Figs. 64:1-3, 65:9-10), and "tend" to exhibit identical variations in shape; (5) the underleaves are in both cases divided into several primary laciniate divisions; in both cases they may be rudimentary (see discussion on p. 91. Herzog (*loc. cit.*, p. 74) describes those of the type of *P. guilleminiana* as "meist ganz rudimentär and unscheinbar," but states that with respect to the degree of development of the underleaves there are recognizable "recht wechselnde Verhältnisse. . . Schon an dem Montagne'schen Original lassen sich die hier allerdings rudimentären Amphigastrien nachsweisen und gleiches gilt von den meisten brasilischen Belegen . . . wie auch für die uns vorliegenden ecuadorischen Pflanzen." Herzog emphasizes that the underleaves are mostly in the form of "winzigen, unregelmässig zerschlitzten Gebilde" and states that they are absent on branches and are not uniformly demonstrable even on the main stems. Although the large majority of collections of typical *P. ludoviciana* possess conspicuous and plurilaciniate underleaves, the underleaves may be small and difficult to demonstrate in some of the plants from our area, *e.g.*, in *Schuster* 22986, 22987 (Fig. 66:17), and in *Schuster* 22975 (Fig. 64:6); even in the type (Fig. 63:2, 9) the underleaves may be locally rudimentary, although usually readily demonstrated. In those plants (*e.g. Schuster* 22986) where the underleaves are reduced to two or three minute, filiform vestiges to 500-600 μ long, the other characters of the species are strongly deviant. It is possible that taxonomic segregation of these variants will prove necessary. Herzog (*loc. cit.*, p. 75, Fig. 12a-b) emphasizes that in some Ecuadoran phases of *P. guilleminiana*, which he segregates as a var. *grandistipula*, the underleaves may be of "ungewöhnlicher Grösse und mannigfaltiger Gestalt."

I have examined a perianth-bearing specimen assigned to this form by Dr. Herzog (Ecuador: Prov. Santiago-Zamora, Patuca, 600 m., *Karling* 2287! *leg.* Herzog). The underleaves here are usually vestigial, and the term "*gran-*

distipula" appears unwarranted, at least by comparison to the "normal" condition in *P. ludoviciana*. These plants, which have the dentition of the leaves and bracts very closely similar to that of typical *P. ludoviciana*, hence coarser than normal for *P. guilleminiana*, diverge from *P. ludoviciana* in one other respect, aside from the reduced underleaves: the perianths are very sharply and often widely winged dorsally, the wing often complete and bearing several teeth above. (This is, apparently, never the case in our *P. ludoviciana*.) Inversely, a specimen from the Herzog herbarium (Brazil: Paso Alegra, *Hoehne*, 1927) labelled simply *P. guilleminiana*, which is very similar in leaf form, size and dentition to the preceding one cited, has much more readily discernible underleaves. Although these are shorter than in *P. ludoviciana* (usually 200-500 μ long), they are similarly divided to near the base into 2-4 major laciniform lobes that range from 4-8 cells broad at base; these lobes are short and soon resolved into several short cilia, each normally ending in a slime papilla. Similar underleaves occur frequently in "*P. guilleminiana* var. *spinosissima* Herz." in a Bolivian plant (Tolopolo near Coroiro, 1300 m., *Buchtien*, 1912). The underleaves, in both of these plants, in view of the optimal size of the plants as a whole, are still much smaller than in *P. ludoviciana*. More normal is the condition in Brazilian plants (Morro de Taragua, S. Paulo, *Hoehne*, 1921), in which the underleaves are vestigial and consist of several minute, filiform laciniae only 2-3 cells wide at base.

Thus, from an examination of a series of specimens of various phases of *P. guilleminiana*, as well as of the type material of the presumed synonyms, *P. oreocharis* and *P. rhizophila*, there emerges a definite impression that the ventral merophytes in these plants are greatly reduced and the underleaves in general very small. Even in plants where they are distinct they are very short and fail to attain a length over 0.3-0.4 the maximal leaf width.

This contrasts strongly with the "normal" condition in *P. ludoviciana*, in which the normal phases have underleaves 0.5-0.9 the leaf width, see *e.g.*, Figs. 61:8, 63:12, 65:5-7, 15-16, 66:8 and 68:22. As a consequence we must conclude that there exists in both the South American *P. guilleminiana* and the North American *P. ludoviciana* broad variation in underleaf form and size, suggesting a very immediate genetic relationship between the two, but the range of variation in the two taxa is clearly quite different. The two "species" also agree closely in the evident tendency for the perianths, whether juvenile or nearly mature, to have the mouth oblique and the postical keel abbreviated in length (compare Herzog's Fig. 8d and 9c with my Figs. 61:2, 64:7, 65:3-4). Such a comparison will also show that the wide differences in form of the cilia or laciniae of the perianth-mouth of *P. ludoviciana* easily suffice to encompass the apparently more limited variation, in this respect, of the forms of *P. guilleminiana*. Herzog speaks of *P. guilleminiana* as a "weitverbreitete neotropische Art" that "zeichnet sich durch eine ungewöhnliche Vielgestaltigkeit aus." Herzog emphasizes, in addition to the form of the perianth and bracts (which we have already seen to be closely similar to those of *P. ludoviciana*), the leaf form of *P. guilleminiana* as a diagnostic feature, stating that "durchgreifend als Artmerkmal scheint . . . nur der gewellt herablaufende, meist ganzrandige Ventralflügel der Stamblätter

zu sein." He admits for the species, as was already emphasized by Stephani, a wide variability in the size and number of the teeth of the leaves; a similar variability, of course, is one of the marked attributes of our *P. ludoviciana!* Although the type of *P. guilleminiana* (see Herzog, *loc. cit.*, Fig. 6a) is only sparingly provided with short, triangular teeth in the distal one-fourth of the leaf Herzog figures (Fig. 8) a fo. *spinosissima* with much sharper teeth, extending down along the postical leaf-margin to within one-fifth of the leaf-base. The nearly edentate type plant can be nearly matched in North American plants (compare Figs. 65: 1-2, 5-8 and 68:22); the mod. *spinosissima* of Herzog is a very close approximation, in dentition, to the type of *P. ludoviciana* (Figs. 63:2-3, 7-9, 67:1)!

Although a very close affinity of *P. ludoviciana* with *P. guilleminiana* is easily demonstrable, the nature of the relationship of *P. ludoviciana* to the South American *P. oreocharis* Spruce and *P. rhizophila Spruce* is open to question. I cannot, at the moment, express full satisfaction with Herzog's (1952) treatment of them, based on Stephani (1905), as simple synonyms of *P. guilleminiana* — and thus possibly conspecific with our *P. ludoviciana.* According to Herzog's figs. 7a and e, the postical leaf bases tend to be less developed and somewhat less decurrent, and the leaves "tend" to be broader in *P. oreocharis* than normal in the *P. guilleminiana-ludoviciana* complex. I, therefore, initially questionably placed these plants into synonymy under *P. guilleminiana.* Questionable also is the attempt to equate *P. oreocharis* with the *P. guilleminiana-ludoviciana* complex, on the basis of Herzog's figures. The former species appears to differ, as is clear from Herzog's figures, in both the armature of the perianth-mouth, and shape of the perichaetial bracts. The perianth appears armed in *P. oreocharis* with only some 13-14 long, spinose teeth on each side or lip of the mouth, according to Herzog's figure; in *P. guilleminiana* Herzog shows varyingly 22, 15 and 29 teeth; in *P. ludoviciana* there are 18-20 or 28-34 cilia or teeth per lip. Similarly, the female bract of *P. oreocharis* is shown by Herzog (fig. 7c) to be very broadly ampliate, while those of *P. guilleminiana* are shown to be more ovate (Figs. 5e, 8c, 9b) and agree more nearly with those I illustrate under *P. ludoviciana.*

However, careful study of the type plants of *P. oreocharis* shows the following divergences from Herzog's figures, and equally well, a marked similarity to *P. ludoviciana* in these features: (1) the leaves are very long-decurrent postically, to 0.7-0.85 or even 0.9 the merophyte length on mature shoot-sectors; this decurrent strip is even longer and more undulate than is normal in most forms of *P. ludoviciana;* (2) the leaf shape varies from broadly ovate-triangular to simply ovate-triangular, and agrees perfectly with the type of *P. ludoviciana*!; (3) the perianth-mouth is armed with 26-30 acuminate laciniae, similar to those shown by Herzog for *P. guilleminiana,* and similar to those I have drawn for *P. ludoviciana* var. *invisus*!; (4) the antical perianth keel is either lamellate and entire, or very broadly lamellate, with the upper end of the lamella ending in 4 close spinose teeth! On the basis of these observations there is nothing to keep these plants apart from *P. ludoviciana,* except that they possess rudimentary underleaves. (The single perianth found bearing teeth on the upper portions of the antical keel may be abnormal. At least such dentition is not usually present in species of this complex). One other point of divergence remains to be noted. In North American *P. ludoviciana* the female bracts usually have the deflexed antical margin entire or subentire, except near the

apex; in *P. oreocharis* the antical bract margins bear a number of spinose teeth or oblique spines. This tendency for more copious dentition of the female bracts is also present in *P. undulifolia* Herz., a plant which I would regard as probably conspecific with *P. ludoviciana*. Surely this feature, *per se*, is insufficient for maintaining these plants as separate species.

Part of the type collection of *P. rhizophila* (from Andes Quitenses: Rio Verde, Pastasa affl.) has been studied in the Yale herbarium. These plants, which are very robust, the shoots attaining a length of 5-6 cm and showing occasional dichotomies, agree habitually with *P. ludoviciana* and are identical in basic leaf-form and dimensions with the type of the latter. They show some variation in degree of decurrence of the postical leaf-base, in some cases it is decurrent for only 0.5 the merophyte length, in extreme cases for up to 0.65 the merophyte length. On this basis they agree with some forms of *P. ludoviciana*, and I would not hesitate to place the plant in synonymy under this were it not for one marked difference: the plants, although as robust as any form I have seen of *P. ludoviciana*, are provided with only vestigial and filiform underleaves. In my experience robust plants of *P. ludoviciana* almost always show perceptible underleaves. For that reason, I have doubts about these plants being conspecific with *P. ludoviciana*, although they cannot be separated specifically from *P. guilleminiana*.

The preceding observations of the types of Spruce's *P. oreocharis* and *P. rhizophila* thus run counter in some respects to the observations and figures of Herzog (*loc. cit.*). On the basis of my study of the types of these species, I can find only one marked difference between them and *P. ludoviciana*, namely the rudimentary underleaves. Spruce's two taxa are identical in this respect, differing from each other chiefly in the degree of postical decurrence of the leaves. In the minute underleaves they also agree with "normal" forms of *P. guilleminiana*.

I have also, independently, studied two plants in the Yale herbarium under the name "*P. guilleminiana*." One plant, from Peru (Santa Anna, *H. W. Foote* 41) is virtually inseparable from the larger phases of *P. ludoviciana*, agreeing in the longly decurrent postical leaf-bases, which are even more undulate than those of our *P. ludoviciana*, and form elongated crests; these plants, furthermore, have distinct, if unusually small underleaves, divided into several ciliary divisions and/or laciniae. The latter are mostly 2, occasionally 3-4 cells wide basally. The other plant, from Bolivia (Prov. Cochabamba, near Incacorral, Jan. 1908, *Th. Herzog*) was determined by Stephani. This plant is extremely robust, but the leaves are more pellucid and lax, narrow and quite falcate, with the leaves narrower and more nearly pointed distally, and with a much abbreviated postical decurrence. They do not, in my estimate, agree with *P. guilleminiana* sensu Herzog (1952), nor with other plants seen referred to that species. These plants do not need to further enter the present discussion, since they prove only that Stephani's concept of *P. guilleminiana* was not sharp, suggesting his observation with regard to *P. rhizophila* and *oreocharis* may not be valid either.

The best, if only temporary, solution to these problems may be to tentatively retain Spruce's two taxa as varieties and to only tentatively

equate *P. guilleminiana* s. lat. with *P. ludoviciana* s. lat. Since the type specimen of the former has not been studied, any nomenclatural changes, especially the reduction of *P. ludoviciana* to synonymy, should remain in abeyance. This situation is rendered more complex by the fact that all of the South American collections in this complex which I have studied are uniformly free of propagula, and neither Herzog nor Stephani mention them for *P. guilleminiana*. This is possibly owing to the fact that the *P. guilleminiana* complex in South America is restricted to wet, deeply shaded forests ("Bergwald" in many cases), and hence the stimulus needed for propagulum-production (presumably strongly fluctuating moisture conditions and intermittent drought) do not obtain. The following key, then, must be regarded as a temporary attempt at a solution:

1. Underleaves usually well-developed, of several laciniae up to 4-10 cells wide at base, their length up to 0.2-0.5 that of lateral leaves; lateral leaves almost constantly with abundant propagulum-production (except in leptodermous shade extremes). ..... *P. ludoviciana* s. str.

1. Underleaves usually vestigial and, if discernible, usually of cilia or laciniae usually only 2-3 (4-6) cells wide at base, less than 0.15 the leaf-length; leaves never producing propagula. (*P. guilleminiana* s. lat.) 2

2. Leaves postically with the decurrence extending for 0.5-0.6 (0.65) the merophyte length. ..... *P. guilleminiana* var. *rhizophila* (Spruce) comb. n.

2. Leaves postically with the decurrent strip very long, gradually and acuminately narrowed, extending down for 0.7-0.85 (0.9) the merophyte length. ..... *P. guilleminiana* var. *oreocharis* (Spruce) comb. n.

The type of *P. guilleminiana* should be checked against the preceding key in order to adjust the above nomenclature. Presumably it will be found to be identical with var. *oreocharis*, in which case the latter can be relegated to synonymy.

The writer has also had the privilege of studying the type of *P. undulifolia* Herz., through the kind cooperation of Dr. Th. Herzog. This species was based on material from Hacienda Simaco, on the road to Tipuani, Bolivia, *ca.* 1400 m (*Buchtien*). The plants are almost identical with typical *P. ludoviciana*, and differ from this merely in (a) reduced underleaves; (b) the leaves frequently with the teeth rather strong to within a short distance of the edentate basal one-fifth of the postical margin; (c) female bracts with the antical, recurved, margin spinose-dentate almost to the base. These differences do not warrant a distinct species. The first two of these differential features are relative characters, occasionally almost equally developed in *P. ludoviciana* from the southeastern United States. It is very doubtful if the more copious development of spinose teeth of the antical margin of the bracts necessitates recognition of *P. undulifolia* as a separate taxon. I would regard it as a form of *P. guilleminiana*. At best, one might conceivably justify recognition of it as a separate variety on the basis of the freely spinose-dentate antical margin of the female bracts.

In addition, a number of specimens have been seen that are referable to *P. ludoviciana* from Cuba: Sierra de las Yeguas, San Diego de los Banos, Prov. de Pinar del Rio (*Leon* 524!), male plants with unusually narrow leaves; no loc. data (Hepaticae Cubensis Wrightianae; type of *P. tunarum* Steph.!); no loc. data (Montagne herb., in NYBG). Inversely, the plants reported by

Evans (1911, 1918) as *P. ludoviciana* from the Bahamas and from the Virgin Islands all represent *P. hypnoides*. If true *P. ludoviciana* is dispersed through the West Indies, outside of Cuba, it is evidently rare there.

P. ludoviciana s. str. is distributed over the entire low-lying por-

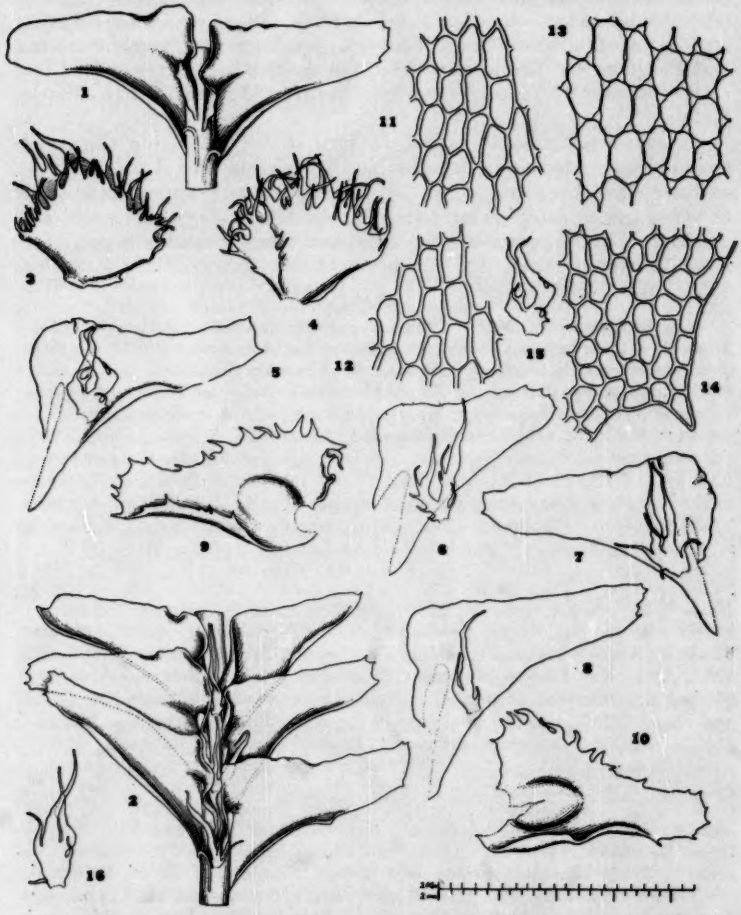

Fig. 65.—*Plagiochila ludoviciana* var. *invisus* Schuster. 1-2. Shoot-sectors, postical aspect (x 16.9); 3-4. Juvenile perianths, antical keels at right (x 16.9); 5-8. Leaves, with adjacent underleaves (x 16.9); 9-10. Female bracts (x 16.9); 11-12. Cells of postical, decurrent base (x 186); 13. Cells of base, along leaf midline (x 186); 14. Cells of leaf apex with tooth (x 186); 15-16. Underleaves (x 186). (All from type material from Pineola, Florida, *Sharp;* figs. 1-10 drawn to bottom portion of scale; 11-14, drawn to top portion of scale.)

tions of the Coastal Plain, from extreme coastal North Carolina southward to tropical Florida, westward along the Gulf of Mexico to eastern Texas; also in the West Indies. The species becomes relatively rare as the Piedmont is approached, but reappears at the edge of the Appalachian Plateau in Georgia, North Carolina, and South Carolina, being found as far inland as Tallulah Falls, Georgia (*Schuster* 34362) and in northwestern South Carolina, southwestern North Carolina, and southeastern Tennessee, where the species becomes localized and rare. Apparently lacking elsewhere in the old Appalachian Plateau region.

Numerous specimens have been seen in herbaria from the Appalachian system from Virginia to North Carolina and Tennessee. All of these have been found to be misdetermined, representing either *P. yokogurensis* subsp. *fragilifolia*, *P. virginica* or *P. virginica* var. *caroliniana*. The reports of this species from the Appalachians and Piedmont of these states (in Blomquist, 1936; Sharp, 1939; Patterson, 1950) must all be deleted.

NORTH CAROLINA: Near Wilmington, Brunswick Co. (*Patterson* 1420!); 3 mi. E. of Scuppernong, 30 ft., Washington Co. (*Anderson* 3983!; northernmost report); shale bluffs of Hiawassee R., Cherokee Co., 2000 ft. (*Anderson* 8077); also reported from six North Carolina counties by Blomquist (1936); all these reports referable to *P. yokogurensis fragilifolia* or *P. virginica*. TENNESSEE: Rabbit Creek, Lake Calderwood, Blount Co., 975 ft. (*Sharp* 3916!; the only previous correct Tennessee report!); Oconee R., above Reservoir, on Rte. 64, 3.4 mi. E. of jct. with Rte. 30, 14 mi. W. of Ducktown (*Schuster* 39513). SOUTH CAROLINA: Gorge of Estatoe R., N. Pickens Co. (*Schuster* 37676, 37669a); Charleston (*Fox*, 1918; *fide* Frye and Clark); Whitewater R. gorge, 0.2 mi. above bridge below Lower Falls, Oconee Co. (*Schuster* 40902, 40903). GEORGIA: Tallulah Falls, Rabun Co. (*Schuster* 34362, 34362a, 34377, 34380, 34380a); Thomasville, Thomas Co. (*Brown*!); Athens, 600 ft. (*R. M. Harper* 59b; *Harper*, June 26, 1900!; fo. with broad, entire-margined leaves); Coffee Co. (*R. M. Harper* 1448b!); no data (*Sullivant*, 1845!, NYBG). FLORIDA: Timm's Hammock, Dade Co. (*Small, Mosier* 52826, 5292, 5290a, 5282, *p.p.*); Hattie Bauer Hammock, Dade Co. (*Small and Mosier* 5297, *p.p.*, 5304, *p.p.*; both with androecia!); Nixon-Lewis Hammock, Dade Co. (*Small and Mosier* 5247, male!); Apalachicola R., Alum Bluff, Liberty Co. (*Schuster* 33537); dry coral limestone grottos at Pineola, Citrus Co. (*Schuster* 37229b, c. ♀, ♂ caps.; 37231, c per.; 37230a, narrow-leaved, xerophytic phase; c. per.; 37213, c. per., forma with largely erect-spreading leaves); Glen Julia, Gadsden Co. (*Schornherst* 2259!), Goodburn Hammock, Dade Co. (*Small and Mosier* 5233; plant superficially transitional to *P. hypnoides*); Snapper Creek Hammock, Dade Co. (*Small and Mosier* 6240!; the *"P. tunarum"* extreme); Sykes Hammock, Dade Co. (*Small, Mosier and Small* 5260!; the *"P. tunarum"* extreme); Ocala, Marion Co. (*Underwood* 1897 *pp.*, with *Euosmolejeunea clausa*); Lake City (*F. C. Straub* 107!); Snapper Hammock, Dade Co. (*E. G. Britton* 410, 501; *"P. tunarum"* extreme, ± leptodermous and shiny); Snapper Creek, S. of Coconut Grove (*Small and Nash* 465! c. per.; mod. *integrifolia-leptoderma*, near *"P. tunarum"*); Old Rhodes Key (*Small and Nash* 494; c. per.; mod. *integrifolia-leptoderma*, near *"P. tunarum"*); Royal Palm Hammock, Collier-Seminole S.P., Collier Co. (*Schuster* 20269, 26128, 26129, 26178a, 26125); 2 mi. SE. of Brooksville, Hernando

Co. (*Schuster* 22730a); Mathesson Hammock, on Old Cutler Rd., S. of Coral Gables, Dade Co. (*Schuster* 22689); Hillsborough State Park, Hillsborough Co. (*Schuster* 33905b, 33930b, 33901, p.p., among *P. aspleniformis, Lejeunea floridana;* 33905a, with *P. floridana, P. aspleniformis*). ALABAMA: Mobile (*Ch. Mohr*!); no loc. (Sullivant, Musci Allegh. No. 223, 1845; part of the type material from Alabama, part from Louisiana); near Chunchulla, Mobile Co. (*Schuster A*-109, *A*-144, *A*-155; c. perianth!; plate). MISSISSIPPI: 8-9 mi. N. of Escatawpa, on Rte. 63, Jackson Co. (*Schuster* 19184, 27833c); on Rte. 57, *ca.* 7 mi. S. of Ramsey Springs, N. Harrison Co., (*Schuster* 27785a, 27766b); 6-7 mi. NE. of Van Cleave, Jackson Co. (*Schuster* 22987, 27791, 22981, 22986, 19211b, 22975, 19242, 19241); Swampy woods, 2-3 mi. N. of Escatawpa, Jackson Co., (*Schuster* 27751a); Wyatt Hills, 15 mi. E. of Perkinston, George Co. (*Schuster* 20198, 27689a; Wyatt Hills, NE. of Ramsey Springs, W. George Co. (*Schuster* 27690a, 27710b, 20199, 26796a); Wyatt Hills, NE. of Ramsey Springs, George Co. (*Schuster* 26594c); Swamp along Black Creek, 7-8 mi. N. of Escatawpa, Jackson Co. (*Schuster* 29234, 29240a). ARKANSAS: Camp Albert Pike, Little Missouri R., N. of Langley, Ouachita Mts., Montgomery Co. (*Anderson* 11390a). LOUISIANA: no loc. data (Sullivant, Musci Allegh. No. 223, 1845, *the type;* in part from material from Alabama); no loc. data (Drummond, Musci Amer. No. 160! 1828, as *Jungermannia spinulosa*); Sulphur Springs near Covington (*Pennebaker,* July 2 1939!, as *P. ludoviciana;* includes almost entirely *P. dubia,* but 1-2 stems of *P. ludoviciana* admixed); Covington (*A. B. Langlois* 381!; admixed with *P. miradorensis*); Fricke's Cave near Folsom, St. Tammany Parish (*Mackaness B*-2, as *P. floridana*); 1 mi. W. of Robert, Tangipahoa Parish (*Correll* 9299, *p.p.,* among *Metzgeria myriapoda, Euosmolejeunea duriscula, Ceratolejeunea laete-fusca*).

Ecology.—Northward, *P. ludoviciana* is most frequently a species of the lower portions of tree-trunks (*Nyssa, Magnolia glauca, Persea, Fagus grandifolia*), usually occurring in the coastal *Magnolia-Persea* Evergreen forests, or in the old *Magnolia*-Beech forests. The species is confined to areas with low light intensity and high humidity (low evaporation rate). It occurs on bark usually up to a height of 4-5 ft. and often forms nearly pure mats near the bases of trees, or even on their exposed roots. The species in most of its area is usually not strictly pioneer in nature, but undergoes ecesis after invasion by the more mesic facies of the *Lejeunea-Radula-Porella* Associule. However, southward, in the tropical hammock forests of Florida, this species becomes ubiquitous and is found in a wider range of habitats. It occurs here on a wide variety of broad-leaved evergreen trees, as well as at the bases of *Taxodium,* the pond cypress. The phenomenal ability of the species to undergo ecesis here is undoubtedly correlated with the abundant production of leafy propagula, which are probably disseminated by raindrops (and possibly in part by gravity). Associated on the bark of trees, on such sites are a wide variety of other Hepaticae, chief among them: *Radula australis, Lejeunea laetevirens, Cheilolejeunea rigidula* and *opaca, Lopholejeunea sagreana, Metzgeria ciliigera* (more rarely *furcata* or *uncigera*), *Ceratolejeunea laete-fusca, Mastigolejeunea auriculata, Frullania squarrosa.* Less frequent associates are (in the area away from the tropical portions of Florida) *Radula*

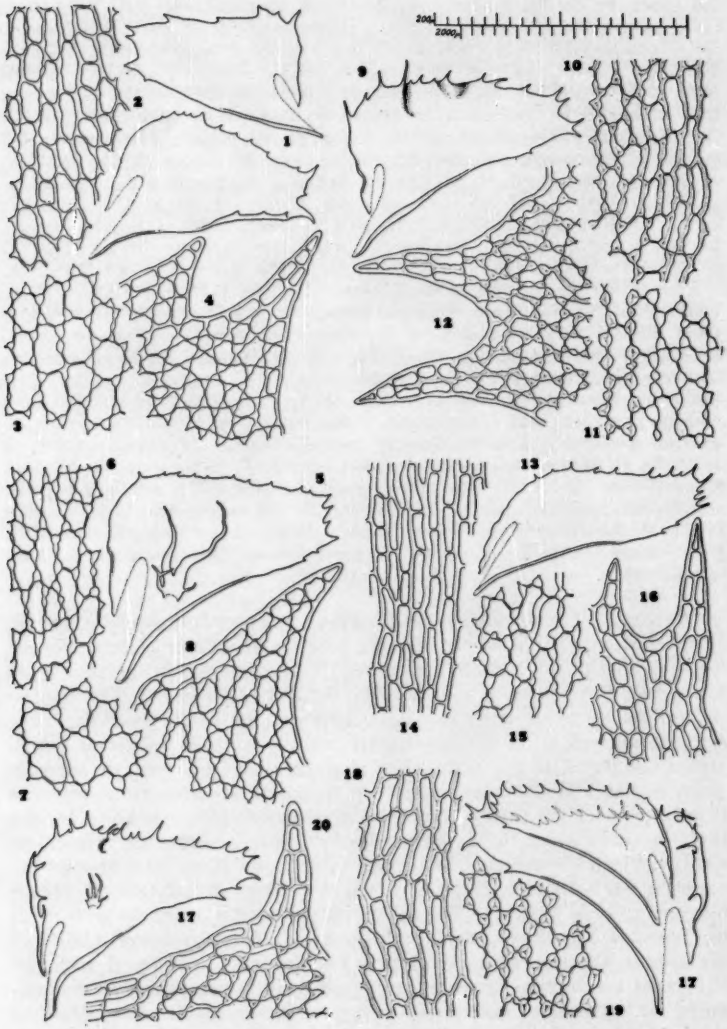

Fig. 66.—*Plagiochila ludoviciana* Sulliv. 1, 5, 9, 13, 17. Leaves and underleaves (x 16.5); 2, 6, 10, 14, 18. Cells of postical base, at origin of decurrent strip (x 182); 3, 7, 11, 15, 19. Median leaf cells (x 182); 4, 8, 12, 16, 20. Cells of leaf-apex (x 182). (Figs. 1-4 from type, leg. *Sullivant* [see also Fig. 63:2-3, 6-9, 11]; 5-8, Chunchulla, Ala., *Schuster* A109 [see also Fig. 61:1-3]; 9-12, N. of Escatawpa, Miss., *Schuster* 19184 [see also Fig. 63:1, 4-5,

obconica, andicola, and *caloosiensis, Neurolejeunea breutelii, Plagiochila undata, miradorensis, dubia* and *floridana, Rectolejeunea maxonii, Harpalejeunea ovata,* and lichens similar to *Chiodecton sanguineum.* In the deep tropical hammock forests of the southern tip of Florida frequently nearly confined to the bases of trees, forming large mats, associated usually with *Radula australis.* Such mats, of shiny, leptodermous plants, are scarcely typical; they represent an extreme form (described by Stephani as *P. tunarum*). In mats various ferns often undergo ecesis, chiefly *Campyloneurum phyllitidis.*

In subtropical and tropical Florida also occasional on shaded, moist banks, on coral limestone (as at Hillsborough R.), then with *Plagiochila aspleniformis* and *Lejeunea floridana.*

At the interior periphery of its range, the species is often saxicolous (as at Tallulah Falls, Georgia; near Murphy, North Carolina; and elsewhere), then occurring on damp to moist, shaded to intermittently sunny rocks in gorges, together with *Porella pinnata, Lejeunea laetevirens, Metzgeria furcata, M. myriopoda, Plagiochila undata, P. asplenioides,* occasionally *Scapania nemorosa* and *Frullania plana,* etc.; rarely *Radula andicola* and *R. voluta* are associated (Oconee R., Tenn.). In such areas the species appears to occur indiscriminately both on bark and on rocks, although more frequent on the latter. The populations from shaded rocks may be quite atypically slender, approaching *P. virginica* var. *caroliniana* in facies.

Differentiation.—*P. ludoviciana* has a distinctive appearance due to the following combination of characters: (1) large size (3-4.5 mm wide) and sparse dichotomous forking, except for innovations; (2) the rather narrow, asymmetrically ovate-triangular, tapering leaves, long-decurrent dorsally, tapering from the dilated base gradually to a narrow, often subtruncate apex that usually bears 3-4 teeth; (3) the nearly straight line formed by the postical margin, above the dilated postical base; the straight distal portion of the postical margin of mature leaves is furthermore normally at almost a right angle to the axis; (4) the virtually constant occurrence of propagula of the postical leaf-surface — usually in exceedingly great abundance; (5) the presence of large, usually bulging trigones; (6) the very dense leaves. These characters are shared, to a large extent, with the allied species, *P. hypnoides, P. miradorensis* and *P. undata.*

The plant, in nature, always occurs as a mod. *densifolia.* This results in a very characteristic appearance when examined ventrally — the dilated postical bases of the leaves are so closely crowded that the postical stem surface is virtually or completely hidden from superficial view (much as in the related *P. undata* and *P. hypnoides,* species which also occur only in the mod. *densifolia*). The postical leaf-bases are furthermore usually erect, often broadly reflexed, usually quite decurrent, and therefore form two approximated lines,

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of admixed *P. miradorensis*]; 13-16, *Schuster* 22986 and 17-20, *Schuster* 22987 [see also Fig. 62:1-3]; all leaf and underleaf figures drawn to bottom portion of scale; all cell figures drawn to top portion of scale.)

or crests, on the ventral stem surface. In material not typically developed, this feature is less apparent, and on branches, or on impoverished plants, the leaf-bases may be much as in the less derivative species, *P. hypnoides,* leading easily to confusion with the latter.

When robust and typically developed, easily separable from the somewhat similar *P. hypnoides* by the laciniate underleaves and by the longly decurrent postical leaf-base, which is usually erect (spreading away from the postical stem-surface at right angles). In this, *P. ludoviciana* exhibits affinities with *P. undata,* from which it differs at once in (1) the more or less coarsely dentate leaf-apex and postical leaf-margin (the teeth usually extending down near to the decurrent base on some leaves); (2) the sinuous or nearly plane, never strongly undulate postical leaf-margin of sterile plants; (3) the almost invariable occurrence of asexual reproduction through the development of brood plantlets from the lower leaf-surfaces (Fig. 64:4); (4) narrower leaves. At times the species occurs under atypical conditions, or in juvenile forms, which are difficult to recognize. Such forms may have the postical leaf-base less decurrent, and not or only narrowly reflexed (Fig. 62:10). Such forms must be separated from *P. hypnoides* with extreme care.

Although *P. ludoviciana* is very similar in some respects to *P. hypnoides* and *P. undata* (and has been widely confused with these two taxa in American herbaria and literature), it has been even more universally confused with *P. miradorensis,* a species which is often fully as common in the outer Coastal Plain as is *P. ludoviciana.* The separation of the two species, is, however, usually easily affected (see the detailed discussion under *P. miradorensis*). *P. ludoviciana* can usually be separated from *P. miradorensis* on the basis of (a) absence of a postical, reflexed-convolute pocket at the base of the leaf; (b) absence of dentition of the basal fourth of the leaf; (c) tendency for the cells at and just above the postical, decurrent strip of the leaves to be strongly elongated and more or less thick-walled on their longitudinal walls; (d) the laciniate underleaves, with the major divisions, at least, a number of cells broad towards base; (e) the edentate dorsal keel of the perianth; (f) the much less elongated perichaetial bracts.

There is also danger of confusing the weak, relatively short-decurrent leaved juvenile extremes of *P. ludoviciana* with *P. virginica* and its var. *caroliniana* Schuster. The writer has seen a considerable number of collections of *P. virginica* var. *caroliniana* in herbaria, under the name of *P. ludoviciana.* However, the pattern of modification of the two taxa is very different. The latter does not produce brown modifications with yellowish confluent trigones, while the xeromorphic phases of the former are brown and extremely strongly collenchymatous-celled. Furthermore, mature shoots of *P. ludoviciana* can always be recognized by the much denser leaves, with the dilated postical bases so shingled that the postical face of the stem is quite hidden from view; in *P. v. caroliniana* the leaf-bases never obscure the stem from below, nor is there any development of a crista.

A characteristic feature of this species is the almost invariable, and abun-

dant, occurrence of asexual reproduction by means of the development of small plants from the lower leaf-surfaces (Fig. 64:4). This is well-indicated in the type material (Fig. 63:7), and occurs in nearly all collections I have examined, which are at all adequate. Although the same type of asexual reproduction occurs in a wide variety of our other *Plagiochila* species, reproduction by leafy propagula is either of more sporadic occurrence in these species, or, when widely present, occurs relatively sparsely on each leaf (and has therefore been overlooked in most of our species — no indication of its occurrence being reported in the majority of them).

Variation.—See discussion of the variation patterns in the *P. ludoviciana-miradorensis* complex, on p. 71. In addition to the pattern of modification portrayed in that connection, there appears to be a considerable amount of genetic variation; some of the "species" questionably placed in synonymy under *P. ludoviciana* probably represent tropical vicariads (see p. 89-94). In spite of the immense variability regionally, both in leaf-shape, dentition, size of the underleaves, form and dentition of the female bracts, and dentition of the perianth-mouth, it seems impractical to recognize formal varieties, among the southeastern populations of the species, with the sole following exception:

Plagiochila ludoviciana var. **invisus** var. n.[2]
Fig. 65

Plantae in medio facie inter *P. ludoviciana* et *P. miradorensis;* folia angusta, subfalcata, apicibus attenuatis, 1.8-2.0 × longis quam latis; margines foliorum vere edentatae; postia lamina decurrens foliorum cellularum vix elongatarum; amphigastria maxima, laciniato-ciliata. Typus: Pineola, Citrus Co., Florida (*A. J. Sharp,* Dec. 16, 1948).

Plants rather robust, pale green, 3.1-3.7 mm wide. Stems 230-300 μ wide. Leaves densely imbricate, *narrowly, subfalcately, ovate-triangular, the distal portions prominently drawn out* (much as in "normal" phases of *P. miradorensis*), up to 1000-1100 μ wide at the ampliate base x1825-2050 μ long (length usually 1.8-2.0 × width); antical margin weakly concavely arched, very prominently long-decurrent, entire-margined to the apex; postical margin *very strongly ampliate and dilated above the decurrent* base, the decurrent base rather broad, *erect and forming a crista or slightly* (*and obscurely*) *reflexed,* not forming a discrete water-sac or basal fold; *leaf-margins virtually edentate,* the region above postical base entire, the postical margin entire to somewhat sinuous, *the* ± *narrowly truncate apex bearing* 1-3 *low and obscure teeth.* Cells moderately collenchymatous, the walls tending also to be equally thickened; apical cells *ca.* 17-20 μ wide x 23-28 μ long, *tending to be nearly equally thick-walled, little elongated;* cells at median base thinner-walled and with sharper, more salient trigones (22) 24-26 μ wide x 33-42 (52) μ long; cells of, and just above, the decur-

[2] The varietal name *invisus* meaning hateful or detested, a reflection of the author's reaction to the discovery of this taxon, which occupies a puzzling and problematical intermediate position between *P. ludoviciana* and *P. miradorensis.*

rent postical strip *virtually equally thick-walled, but only moderately elongated, ca.* 18-22 (23) μ wide x 30-35 (38) μ long, averaging less than twice as long as wide. *Underleaves very large,* to 1000-1150 μ long, of 2 major, tortuous, lanceolate-acuminate divisions, armed with basal and subbasal lateral cilia.

Female bracts very strongly ampliate above postical base, strongly narrowed towards the narrow, subtruncate apex; ampliate postical margin *coarsely dentate* with broad based, often irregularly bent, variously directed, *acute but scarcely sharp teeth,* distal half of bract and its apex with a few smaller but sharper teeth; antical margin revolute to the apex, with usually 3-5 sharp but small teeth of the distal 0.5-0.75 of the margin. Perianth (juvenile) with mouth coarsely and longly laciniate-ciliate, some of the divisions 3-6 cells wide at base, or more; the longer antical keel with a narrow but sharp wing in the basal half, which may gradually become vestigial above or end in an obtuse to subacute tooth.

Type.—Pineola, Citrus Co., Florida; on bark of *Sapindus* (*A. J. Sharp,* Dec. 16, 1948). The type was determined as *P. undata* Sulliv. by Redfearn, and formed the basis for the report of this species from Citrus Co., Florida in Redfearn (1952). Plants connecting this variant to typical *P. ludoviciana* are those of *Schuster* 33901, from Hillsborough R. State Park, Florida.

Differentiation.—*P. ludoviciana invisus* is a plant occupying a disturbingly intermediate position between *P. ludoviciana* and *P. miradorensis.* On first glance, it gives the impression of an almost typical form of the latter species, agreeing with it in the following superficial features: (a) rather pale or whitish green color, with slight brownish tinge; (b) rather pellucid cells and leaves; (c) the falcate, long drawn out and slender leaves, narrowly truncate at the apex in most cases, with their margins almost edentate. Under the microscope several other similarities to *P. miradorensis* become apparent, which are equally important: (a) the cells at the base of the long-decurrent postical strip little elongated, not forming a zone of sharply elongated, strongly thick-walled cells; (b) dentition much reduced — virtually lacking on most leaves. The impression the plants give, particularly that derived from the leaf-shape and the subentire leaf-margins, is strongly suggestive of *P. miradorensis.* Yet it is wholly impossible to place this material under the latter species, since it shows these major deviant features: (a) the underleaves are large, laciniate-ciliate, with the major lobes 4-6 cells wide at base or more; (b) the postical leaf-base is elevated as a somewhat crisped and undulate crista, but never shows any marked tendency to be reflexed to form a water-sac; this base of the leaf is entire; (c) juvenile plants (and these are preponderant in the collection) show no trace of a water-sac, and show only a slight tendency towards formation of a crista; (d) the perianths lack distinct teeth of the antical keel.

In some of the preceding features *P. ludoviciana invisus* agrees with typical *P. ludoviciana,* particularly in the edentate antical perianth keel; the total lack of a revolute postical leaf-base (and consequent

lack of a water-sac); the laciniate-ciliate underleaves. On the other hand, *P. ludoviciana invisus* differs from typical *P. ludoviciana* in the (a) lack of cellular differentiation of the postical leaf-base; (b) in the virtually edentate leaves, although extreme shade forms of typical *P. ludoviciana* may have almost edentate leaves; these quite fail to develop the mature aspect which the fertile plants of *P. ludoviciana invisus* possess; they also have much more abbreviated leaves, not at all falcate in form; (c) in the falcate and drawn-out distal portions of the leaves; (d) in the lack of any marked tendency for the cells of the leaves to become prominently elongated at the leaf tips. These differences seem slight, yet cannot be reconciled with the broad pattern of variation exhibited by "normal" *P. ludoviciana.* It is particularly impossible to reconcile the facies of these plants, which is totally that of *P. miradorensis,* with the *P. ludoviciana*-like underleaves and form of the postical leaf-bases.

The type material has been confused with *P. undata.* Although the crispate basal portions of the postical margins of the leaves might suggest *P. undata,* no immediate relationship to that species is possible. The narrow, attenuated leaves are quite unlike those of *P. undata* (although their subentire margins suggest those of *P. undata*). *P. undata* differs further in the broadly winged and dentate antical keel of the perianth.

PLAGIOCHILA MIRADORENSIS Gottsche

Figs. 61:4, 5; 62:6-7; 63:1, 4-5, 10; 67:6-18; 68:1-21; 69; 70

Plagiochila cucullata var. *b* Gottsche, Lindenb. and Nees, Syn. Hep. 642, 1847. *Plagiochila miradorensis* Gottsche, Mex. Leverm. 127. pl. 10, figs. 1-10, 1863. *Plagiochila ludoviciana* Evans, Bot. Gaz. 21:192, 1896 (p.p; at least as to figs. Pl. 16, figs. 5-7, 12); Kurz and Little, Bull. Fla. State College for Women 24(3):34, fig. 48, 1933 (at least p. part); Frye and Clark, Univ. Wash. Publ. Biol. 6(3):454, figs. 2, 5-6, 8-9 (in part).

Plants in robust patches, pale green to somewhat olive green, the aerial shoots ascending, simple or sporadically pseudodichotomously furcate; shoots 2.8-3.8, occasionally to 4.75 mm wide, rather robust; stems 200-300 μ in diameter, commonly yellowish-brown, rather rigid. Leaves *closely imbricate, extremely polymorphous,* varying from narrowly *ovate-falcate to lanceolate-falcate* or even rectangulate-falcate, from a minimum of 1580 μ long x 840 μ wide to a median figure of *ca.* 1875-2100 μ long x (850) 900-1050 μ wide, occasionally to 2250-2450 μ long x 1075-1475 μ wide; *leaves with base erect and sheathing when dry* (*only the* $\pm$ *convolute and twisted distal, narrow "limb" strongly laterally spreading*); when moist laterally spreading from *ca.* a 45-55° angle, at base, to a 90-100° angle in the distal half of the leaf; postical margin at usually *ca.* a 90-100° angle with stem; *postical margin ampliate above the long-decurrent base,* the distal two-thirds of the postical margin nearly straight or slightly falcately arched, subparallel to distal portion of antical margin, or gradually convergent to it; *postical base rather broadly dilated* (including the decurrent por-

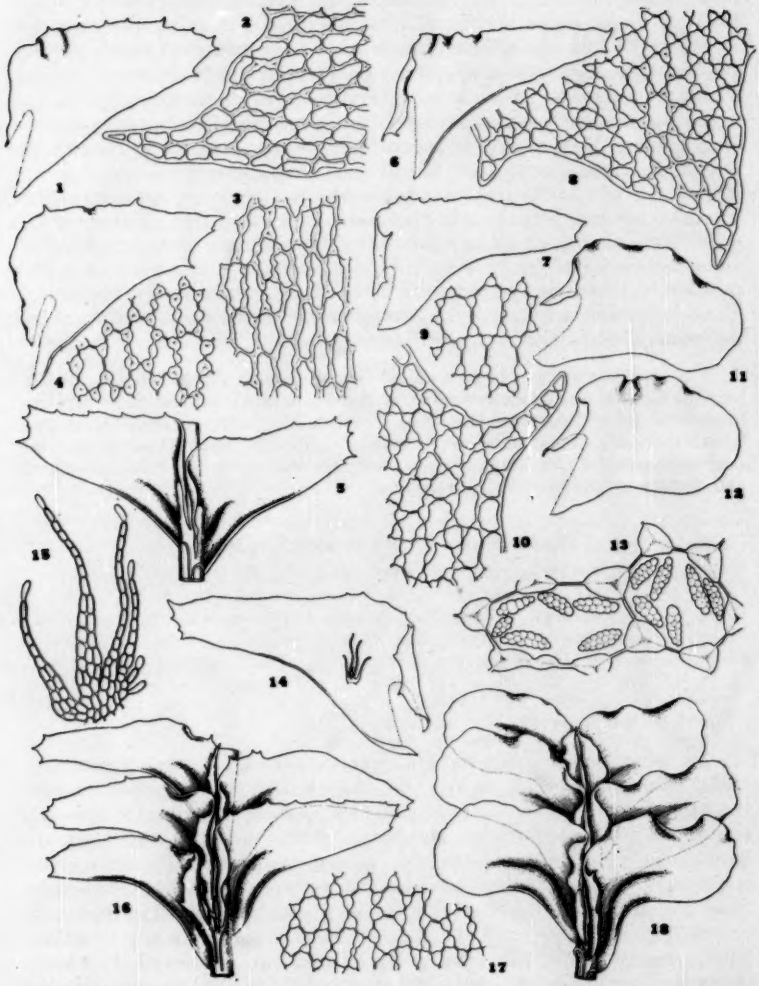

Fig. 67.—*Plagiochila ludoviciana* Sulliv. and *P. miradorensis* Gottsche, from plants growing admixed. 1-5. *P. ludoviciana.* 1. Leaves (x 16.5); 2. Cells of leaf-apex (x 182); 3. Cells of postical leaf base (x 182); 4. Cells from base of leaf near middle of leaf (x 182); 5. Shoot-sector, postical aspect (x 16.5). *P. miradorensis.* 6-7. Normal leaves (x 16.5); 8. Leaf-apex cells (x 182); 9. Cells of leaf base along midline (x 182); 10. Cells of leaf at and just above postical decurrent base (x 182); 11-12. Atypical leaves (x 16.5); 13. Median cells with oil-bodies (x 635); 14. Leaf and underleaf (x 16.5); 15. Underleaf

tion), *long-decurrent* (for usually 0.55-0.75 the merophyte length), the decurrent strip and basal portion above it *strongly reflexed-convolute, the free margin often ± involute* (and thus not exposed to view), forming a somewhat tubular water-sac; antical margin reflexed for usually the basal 0.5-0.7, normally somewhat arched, but in extremely narrow-leaved forms often almost straight. Leaf-margins variable, but the *teeth always less sharply developed, and fewer than in P. hypnoides, usually much less sharp (and often fewer) than in P. ludoviciana;* apex commonly obliquely truncate, the angles of the truncation marked by 2 low teeth, of which the lower may be obsolete (the leaf then merely obliquely acute at tip), more rarely both obsolete, and leaf then rounded at apex; postical margin, above the base, frequently *almost or quite edentate, occasionally with* 2-6 (8-12) *low and weak teeth* (1-3 cells long x 1-2 cells wide at base), the teeth never truly spinose, *broad-based and merely acute,* often reduced to angulations, *or the margin merely sinuate;* postical, reflexed base normally more *sharply and prominently spinose-dentate, or short-ciliate, bearing usually* 1-5 (6) *teeth* (1-several of which may be hidden and involute; occasionally with teeth only 0-1); antical margin edentate, except (rarely) for 1-2 preapical low teeth. Cells always *strongly collenchymatous*: the cells of the leaf-apex and upper leaf-margins *nearly isodiametric,* with coarse, nodular trigones, separated by sharply defined thin regions, the *trigones thus rarely if ever broadly confluent;* apical and subapical cells *ca.* 18-20 (23) μ x 20-25 (27-30) μ; median cells little elongate, with coarse, well-defined trigones, 18-23 x 26-30 (32-38) μ; basal median cells little elongated, with coarse, nodular trigones, occasional intermediate thickenings, 22-27 (32-35) x 30-35 (36-40) μ; cells of the postical, decurrent portion somewhat smaller, strongly collenchymatous (the trigones occasionally somewhat confluent, but *never to the point where the walls become subequally thickened*), *little or moderately elongated* (length: width 1-2, rarely 2.5-1), *ca.* (16) 18-24 x 24-33 μ. Oil-bodies segmented, as in *P. ludoviciana,* commonly 5-8 per cell, *ca.* 3-3.5 x 5-9 (11) μ, formed of (1) 2-3 rows of coarse, protuberant spherules or segments. *Underleaves slender and small, formed of* 2-*several linear, often tortuous cilia that are uniseriate for much or all of their length;* cilia occasionally branched, ending usually in clavate slime-papillae; total underleaf length to 500-975 μ. Asexual reproduction by propagula of the postical leaf-surfaces always present, usually less conspicuous and copious than in *P. ludoviciana.*

Dioecious. Mature perianth oblong-obovate, ca. 2.5 × as long as wide as at mouth, the antical keel narrowly but distinctly winged, the undulate-reflexed mouth freely, but not contiguously spinose-ciliate;

(x 64); 16. Normal shoot-sector from shoot of same plant in fig. 18 (x 16.5); 17. Median cells (x 182); 18. Atypical shoot-sector, postical view (x 16.5). (Figs. 1-12, 14-18 all from *Schuster* 19242, near Van Cleave, Miss.; 13, from Juniper Springs, Fla.; figs. 1, 5-7, 11-12, 14, 16, 18 all drawn to same scale as bottom scale in Fig. 66; figs. 2-4, 8-10, 17 all drawn to same scale as top scale in Fig. 66.)

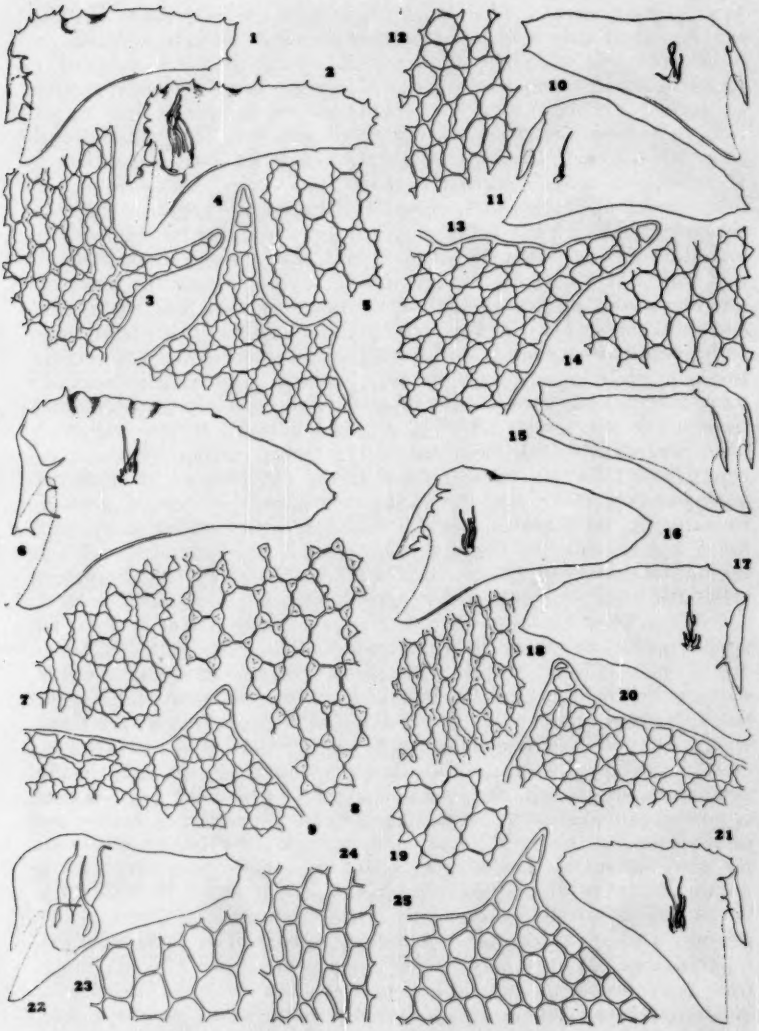

Fig. 68.—*Plagiochila miradorensis* Gottsche. (1-21) and *P. ludoviciana* (22-25). 1-2, 6, 10, 15-17, 21-22. Leaves and underleaves (x 16.5); 3, 7, 12, 18, 24. Cells of postical leaf-bases, just above decurrent strip (x 182); 4, 9, 13, 20, 25. Cells of leaf-apex, showing form of apical teeth (x 182); 5, 8, 14, 19, 23. Cells of leaf base, along midline of leaf (x 182). (Figs. of leaves and underleaves drawn to bottom scale in Fig. 66; figs. of cells all drawn to top scale in

antical wing 2-5 cells wide, extending from base to above middle (sometimes to apex) *bearing* 2-4 *sharp but small teeth;* perianth with the crispate-undulate and ± reflexed mouth quite oblique, the postical keel much shorter than antical. Capsule shortly exserted beyond perianth. Bracts as long as mature perianth, *ca.* 2.3-2.75 × as long as wide, sometimes dentate on the distal 4/5 of the antical margin (at other times with antical margin edentate) as well as on the entire postical margin and apex, narrowed to a subtruncate, narrow apex; bracts from 2400 μ long x 1050 μ wide subbasally (950 μ, with margin inrolled) to 2750 μ long x 1500 μ wide (1300 μ wide with antical margin rolled in), oblong-ovate and somewhat falcate, strongly narrowed distally (width near apex only 350-450 μ).

Type.—Near Mirador, Mexico (*ca.* 3000 ft.) (Liebmann). The type, in the Gottsche herbarium, presumably destroyed. *Neotype.*—Bogue Banks, Carteret Co., North Carolina (*E. Felton Jones* 2596) in herb. Duke University, and of author.

Distribution.—P. miradorensis appears to be distributed very much like the closely allied *P. ludoviciana,* but is much more strictly coastal in range, never occurring at the margin of the Blue Ridge or in the Piedmont. In our area confined to low elevations (below 300 ft., evidently), and occurring only in the outer Coastal Plain, although more widely distributed throughout most of central and northern Florida. To our south extending to Mexico, and very probably considerably farther southward. The range southward is almost impossible to ascertain at present, owing to the taxonomic confusion in this complex. In the United States extending from the Gulf Coast of Texas into Louisiana, Mississippi, Alabama, south to the Oligocene Island area of central (but not to southernmost!) Florida, northward along the Coastal Plain to slightly north of the Cape Hatteras region of North Carolina (where confined to the outermost edge of the Coastal Plain).

NORTH CAROLINA: Hoffman Forest, Bogue Banks, S. of Atlantic Beach, Carteret Co. (*Jones* 2596, neotype! mod. *latifolia-dentata*). GEORGIA: Okefenokee Swamp, Charlton Co. (*Blomquist* 11512!). FLORIDA: Hammock forest 3-4 mi. NW. of Brooksville, Hernando Co. (*Schuster* 22085a, 22110a, 22726a; mod. *angustifolia-dentata;* in part trans. ad var. *convoluta*); hammock forest N. of Gulf Hammock, Levy Co. (*Schuster F*-138, *F*-150; mod. *angustifolia-dentata,* and trans. ad mod. *latifolia-integrifolia*); Glen Julia, Gadsden Co. (*Schornherst* 2259, as *P. ludoviciana!* Most duplicates of this number, each containing only a few stems, are *P. miradorensis;* in one case some true *P. ludoviciana* (NYBG) was admixed); Juniper Springs, Ocala Ntl. Forest, Marion Co. (*Schuster* 31935); Sanford, Seminole Co. (*Rapp;* det. and reported as *P. ludoviciana* by Redfearn, 1953!; *Rapp,* May, 1918 and *Rapp* 31, as *P. ludovi-*

Fig. 66. Figs. 1-5, *Schuster* 22085a, Brooksville, Fla. [see also Fig. 61:4-5]; 6-9, *Jones* 2596, Bogue Banks, N.C. [see also Fig. 69:10-11]; 10-15, type of var. *convoluta* Schuster, *Schuster* 27759, Escatawpa, Miss. [see also Fig. 69:1-9]; 16-21, *Whitehouse* 23318, Texas [see also Fig. 62:6-7]; 22-25, *Schuster* 33901, Hillsborough R., Fla.)

ciana!); DeLeon Springs, Seminole Co. (*Rapp* 14!; as *P. undata,* Y); below Bartow, Polk Co. (*Vanning and Row* 154!); Ocala (*Underwood,* 1837, 1866, as *P. ludoviciana*!); Monticello (*Lighthipe* 26!, as *P. ludoviciana*); Rosewood (*A. P. Garber* 169, as *P. ludoviciana!*); Johnson's Juniper Swamp, 8 mi. S. of Bristol (*Kurz* 40!; with immature perianths); Gainesville, Alachua Co. (*N. L. T. Nelson* 106!). The last two collections served, in part, as the report of "*P. ludoviciana*" from northern Florida (in Kurz and Little, 1933). MISSISSIPPI: Swamp forest 2-3 mi. N. of Escatawpa, Jackson Co. (*Schuster* 19124a, 19250b, 1951; *Schuster* 27759, 1953, the var. *convoluta!*); near Pascagoula R., 6-8 mi. NE. of Van Cleave, Jackson Co. (*Schuster* 19242a p.p., 19213b, 19230e, 22981, p.p. with *ludoviciana*); swamp forest on Rte. 57, NE. corner of Harrison Co. (*Schuster* 2770b); Black Creek, 7-8 mi. N. of Escatawpa, Jackson Co. (*Schuster* 19184a, p.p., with *P. ludoviciana*). (These collections all the mod. *angustifolia-dentata,* but *Schuster* 27759 the var. *convoluta,* and *Schuster* 22981 trans. ad mod. *latifolia-integrifolia*); Biloxi (*Lloyd and Tracy, Sept. 1900!,* as *P. ludoviciana*); Bay St. Louis (*Langlois, Apr. 28, 1885!* as *P. ludoviciana*). LOUISIANA: Fricke's Cave near Folsom, in Magnolia bog (*Mackaness* B-4!, as *P. ludoviciana*); Lafayette (*Langlois* 5151!, 625! as *P. ludoviciana*); Bayue Station (*Langlois* 516!, as *P. ludoviciana*); Chinchuba, Tammany Parish (*Langlois* 620! as *P. ludoviciana*); near Duchamps (*Langlois* 624! as *P. ludoviciana,* Y); Chinchuba, at foot of trees in ravines (*Langlois, Apr. 20, 1891!*). TEXAS: Along creek, 7 mi. S. of Silsbee, Hardin Co. (*Whitehouse* 23318, 24988; mod. *latifolia-integrifolia* and transition to *latifolia-dentata*).

Ecology.—Usually somewhat xerophytic, occurring on dry bark, but also often in rather deep coastal swamp forests, under conditions of persistently high humidity. In our area often on the bases of trees along the slow-moving, sluggish, "black water" creeks along the immediate coast, in forests consisting of *Taxodium,* and the evergreen *Chamaecyparis, Magnolia virginiana, Persea borbonia, Cyrilla racemosa* and *Cliftonia monophylla,* and a few deciduous trees (*Acer rubrum; Nyssa sylvatica biflora*); it has been collected on the bark of the latter two trees. Here it may form large patches, amidst which the rhizomes of the fern, *Polypodium polypodioides michauxiana* grow, as well as the roots of the orchid, *Epidendrum conopseum.* Associated hepaticae, under such conditions, are *Mastigolejeunea auriculata, Cheilolejeunea rigidula* and *clausa, Ceratolejeunea laete-fusca, Radula caloosiensis, R. australis, Lejeunea flava* and *laetevirens, Metzgeria furcata* and *uncigera, Rectolejeunea maxonii,* more rarely *Cololejeunea contractiloba* (which may be ephiphytic on the *Plagiochila*), *Neurolejeunea breutelii,* and *Plagiochila ludoviciana.* The intimate admixture of the latter species (in *Schuster* 19184a and 19242a) is significant in affording us some means of measuring the degree to which these two allied species differ from each other.

The plant also occurs in mixed swamp forests (*Magnolia grandiflora-Ilex opaca-Quercus nigra*), where it has been found on the bark of the *Magnolia,* and on *Liriodendron* and *Quercus nigra,* associated with most of the Hepaticae previously listed. Associated there also with *Plagiochila ludoviciana* (in *Schuster* 22981; on *Q. nigra*). Occasionally also in rich, mixed, subtropical "hammock" forests, on the

bark of a variety of trees. In drier situations, as in partial sun, sometimes admixed with *Frullania squarrosa*. Inversely, occasionally on bark along streams, when mixed with *Porella pinnata*.

Differentiation.—*P. miradorensis* is allied most directly, among our species, to *P. ludoviciana*. It has been consistently confused with this

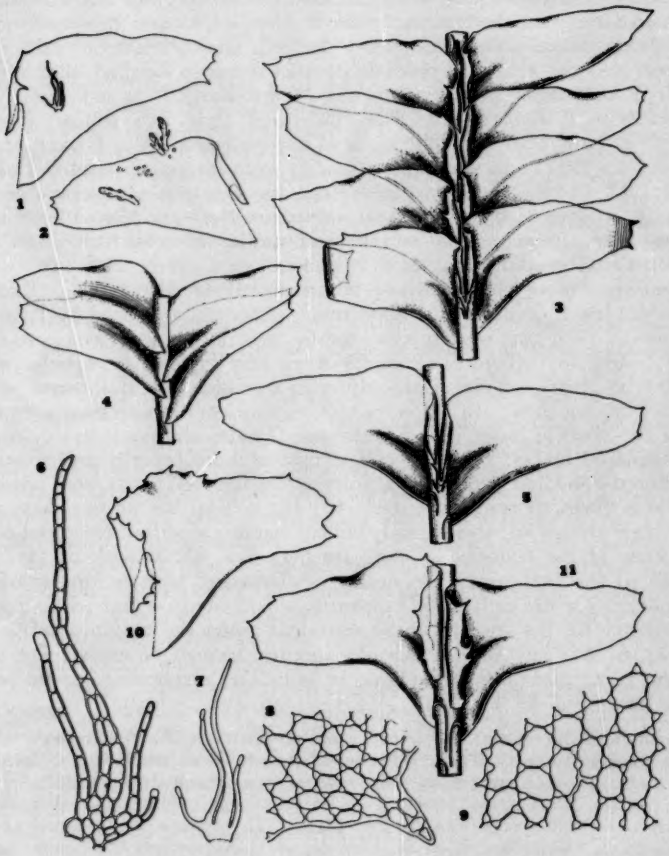

Fig. 69.—*Plagiochila miradorensis* var. *convoluta* Schuster (1-9) and *P. miradorensis* Gottsche (10-11). 1-2. Leaves and underleaf (x 16.5); 3, 5. Shoot-sectors, postical aspect (x 16.5); 4. Shoot-sector, antical aspect (x 11.7); 6. Underleaf (x 57); 7. Underleaf (x 29); 8. Cells near postical leaf base (x 180); 9. Cells near median base of leaf (x 180); 10. Leaf (x 12.4); 11. Shoot-sector, postical aspect (x 12.4). (Figs. 1-9, from type of var. *convoluta Schuster* 27759, Miss.; 10-11, from *Jones* 2569, Bogue Banks, N.C.)

species in all the American literature, starting with Evans (1896), going up to Frye and Clark (1944). For example, part of the cited material in Frye and Clark (*loc. cit.*, p. 454) is true *P. ludoviciana* as are their figures (1, 3-4) of the underleaves, whereas, a part of the cited material represents *P. miradorensis,* while the Virginia plant represents *P. yokogurensis.* The confusion between the two species is based largely on the fact that *both P. ludoviciana* and *P. miradorensis* are exceptionally variable species. Indeed, the variability of each is so great and the ability to produce parallel forms so marked, that I was, for a long time, willing to regard *P. miradorensis* as a synonym or variety of *P. ludoviciana.* The final proof that two distinct species were at hand came with the study of one collection (Van Cleave, Miss., *Schuster* 19242) in which both species were intimately admixed (Fig. 67:1-12, 14-18). In essence, therefore, the two taxa were available for study, *as grown under identical environmental conditions.* Both species were almost equally robust, and similar in color (although the plants of *P. ludoviciana,* as is apparently uniformly the case, were somewhat more chlorophyllose, consequently more opaque). Except for the few *P. undata*-like (abnormal?) extremes produced by *P. miradorensis,* both taxa were represented by "normal" phases (compare Fig. 67:5 and 16). Typical *P. ludoviciana* and typical *P. miradorensis,* when so contrasted, are seen to differ in a considerable number of ways, chief among them: (a) *P. miradorensis* has less dentate leaves, except for the postical bases; (b) it has more falcate, and considerably more attenuated leaves; (c) the postical base is more broadly and strongly reflexed-convolute, forming a tubular "water-sac"; (d) the postical base is distinctly spinose-dentate; (e) the cells of the postical base are scarcely elongated, and strongly collenchymatous, without marked confluence of the trigones — compare here Fig. 67:10 with 3; (f) the cells of the leaf-apices are nearly isodiametric, without any marked tendency for the cells to be tangentially elongated — and without any tendency for the trigones to be confluent along the longitudinal walls (Fig. 67:8); (g) the underleaves minute, formed of usually 2-4 filiform cilia, uniseriate throughout, or only 2 — rarely 3 — seriate near the base (Fig. 67:14, 15).

Of these differences, *c, d, e* and *g* are the most constant and systematically the most important. These differences were fully as marked in a second "mixed" collection, where the two species grew intimately admixed (*Schuster* 19184a, Black Creek, 8-9 mi. N. of Escatawpa, Miss.), and in a third (*Schuster* 22981, near Van Cleave, Miss.). In extreme shade forms of *P. ludoviciana* (which are, however, very deeply chlorophyllose and opaque) the leaves may be as nearly edentate as in "normal" *P. miradorensis* (compare Fig. 68:6, 10, 17 with Fig. 68:22), and have the cells with small or vestigial trigones. The total lack of any dentition of the cristate postical leaf-bases serves to separate such phases of *P. ludoviciana* from all forms of *P. miradorensis.*

Among the many collections of *P. miradorensis* seen from this area, only one (*Schuster* 19250b) possessed mature perianths. The perianths in this case were not fertilized, and the inner faces, and base, had proliferated "propagula" — a feature also often characteristic of the unfertilized perianths of *P. ludovi-*

ciana. The larger perianths seen were *ca.* 1300 μ wide and up to 2200 μ long. In these the antical keel was sharply, if narrowly, winged for almost their total length, with the wing bearing 3-4 inconspicuous teeth. The mouth, as in *P. ludoviciana,* was obliquely terminated, with the postical keel as a consequence shorter than the antical. The ventral half of the mouth was distinctly undulate-reflexed, again a feature typical of *P. ludoviciana.* The perianth thus closely agreed with that of *P. ludoviciana,* except for one feature: the presence of a more discrete, dentate, antical keel, extending upward for all — or almost all — of the length of the perianth. This feature also characterizes the type of *P. miradorensis.*

By contrast, *P. ludoviciana* (and such presumed synonyms of it as *P. schliemiana, P. plicata, P. schiedeana,* and *P. punctualis*) have an essentially or quite edentate antical keel of the perianth. In *P. patula* and *P. subcristata,* which closely resemble *P. ludoviciana* in other respects, the antical keel of the perianth is widely winged, at least below, and dentate. If the latter prove to be discrete species, *P. ludoviciana* may then be considered to include only populations with the perianth-wing poorly developed and edentate, while *P. miradorensis* has the rather well-developed antical perianth wing armed with several small teeth. Study of much longer series of "fruiting" specimens is needed to substantiate such a suggested difference.

Among the neotropical species restricted to Central and South America, *P. miradorensis* appears to be related most immediately to *P. cucullata* Lindenb. et Gottsche (in G. L. et N., Syn. Hep. 642, 1847). This Mexican species is more fully described and illustrated by Gottsche (1863). As Gottsche has indicated, the later described *P. miradorensis* differs from *P. cucullata* in the much smaller underleaves, which are reduced to 2-several tortuous capillary cilia. Our material, referred to *P. miradorensis,* agrees closely — and apparently uniformly — with *P. miradorensis* in the form of the underleaves. This suggests that the large, laciniate and ciliate underleaves of *P. cucullata* serve to separate it from *P. miradorensis* specifically. Gottsche also cited a further difference: *P. cucullata,* in drying, develops "convoluta corrugataque folia"; in *P. miradorensis* they supposedly do not become convolute in drying. Whether this difference is valid or not is not determinable from the material available.

It is clearly necessary to study a series of specimens from Mexico to determine whether these two differences warrant separation of *P. miradorensis* from *P. cucullata.* For the time being, the former is maintained as a distinct species, largely because no intermediates to *P. cucullata* have been found. It may well prove necessary, however, to treat *P. miradorensis* as a mere variant of *P. cucullata* (as was done in the *Synopsis Hepaticarum,* p. 642, 1847).

The appearance of dry individuals of mature plants of our phases of the *P. miradorensis* complex is most characteristic. The basal, ampliate portions of the leaves are erect and closely sheath the stem — with the consequence that the plant superficially appears to have a very stout stem. By contrast, the narrow, slender, drawn-out portions of the leaves are often convolute and twisted, sometimes forming a slender tube. These twisted distal portions of the leaves, in the aggregate, often give the superficial impression of slender, spreading spur-like appendages arising from a thickened axis.

In weaker plants, this characteristic mode of drying is often not as marked. However, the different aspects of dry plants of *P. ludoviciana* and *P. hypnoides* (which have simply postically secund leaves, in drying) and *P. miradorensis* are always easily evident to the practiced eye. On this sole basis, it was possible to consistently separate individual shoots of *P. ludoviciana* and *P. miradorensis*, when the two grow admixed (as in *Schuster* 19184a).

Variation.—An extraordinarily variable species. The pattern of variation is discussed at length (see discussion under Sectio Crispatae), in conjunction with the differences in variation between this species and *P. ludoviciana.*

The variability in leaf form is so extreme that a diagnosis of the leaf-shape must either be so broad as to be meaningless, or else restricted to more or less "typical" manifestations of the species (as has been done above). In extreme cases (Fig. 68:1-2), the leaf apex and postical margin bear from 12-16 sharp but low teeth, in addition to 4-7 cilia-like teeth of the reflexed basal "flap." Such cases are exceptional and approach *P. ludoviciana* in the dentition. The teeth in *P. miradorensis* are usually more distinctly serrate in nature than in *P. ludoviciana.* Those of the postical margin are all, or almost all, distinctly oblique. To a lesser extent this may be true of *P. ludoviciana.* More frequently the leaves have the dentition much reduced, often to 1-3 teeth near the leaf-apex, with the postical margin edentate or merely sinuate, except for the postical reflexed base, which retains

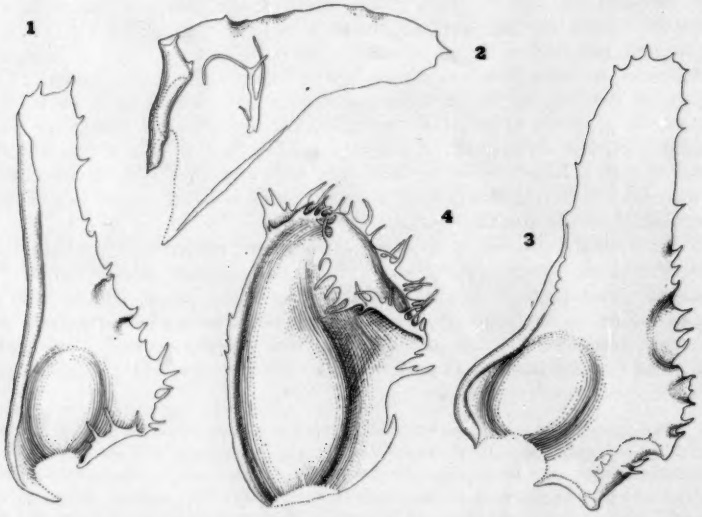

Fig. 70.—*Plagiochila miradorensis* Gottsche. 1, 3. Female bracts (x 21); 2. Stem leaf and underleaf (x 21); 4. Perianth in lateral aspect (x 21). (Figures all drawn from *Schuster* 19250b.)

usually 1-5 sharp teeth (Figs 67: 6-7, 14; 68: 10-11, 15-17). This is to be regarded as the "normal", or at least "common" phase of the species, and is produced under relatively xeric conditions. In both of these forms there is a wide range as to leaf-shape, this ranging from falcate-oblong (Fig. 67:14), with the leaves ca. 1900-2000 μ long x 850-900 μ wide; to ovate-lanceolate (Fig. 68:10-11), with the leaves ca. 1850-2000 μ long x 900-925 μ wide; to relatively broadly ovate-falcate (Fig. 68:6), and up to 2450 μ long x 1475 μ wide. The leaves, in all such forms, are little or not undulate along the postical margin, and are conspicuously, gradually narrowed to the apex. They average consistently from *ca.* (1.65-1.7) 1.85-2.35 as long as wide.

Occasionally, however, totally anomalous phases are produced (Fig. 67: 11-12, 18), in which the leaf is a rounded and abbreviate oblong-lingulate, ranging from 1360-1450 μ long x 1000-1025 μ wide (*i.e.*, only from 1.35-1.45 $\times$ as long as wide!). Shoots with leaves of this type at first glance give the impression of belonging to wholly different species — the leaves being strongly crispate-undulate, with the rounded apices and edentate margins of *P. undata*. However, the transition from this type of leaf to the "normal" type may occur on the same shoot! Fig. 67:6-7 and 11-12 were drawn from leaves of one plant, as were Figs. 16, 18! It is to be noted that the leaf-margins of this anomalous extreme, with broadly oblong-lingulate leaves, are quite entire and broadly rounded at the apex — even the reflexed postical base is usually totally edentate. Why perfectly normal shoots should "go over" suddenly into the oblong-lingulate extreme is not clear. One plant, carefully studied, shows one aerial branch with the leaves consistently of the type in Fig. 67:11-12, 18; on the other aerial branch the basal portion (figured in Fig. 67:16) had similar leaves, with suddenly a cessation of this type of leaf, the distal portions of the shoot showing first short, rudimentary leaves, then "going over" into a sector (illustrated in Fig. 67:18), with leaves strongly reminiscent of those of *P. undata*. A few other shoots, wholly with leaves of this latter type, were also noted.

Only one variant, based on leaf-type, appears sufficiently stable and sharply defined to warrant recognition as a separate variety, var. *convoluta*. This is treated below. Excluding this, the species still remains extremely polymorphous.

Plagiochila miradorensis var. **convoluta** var. n.

Figs. 68:10-15; 69:1-9

Folia tenua, 2.0-2.2 $\times$ longa quam lata, falcata; posticus basis fere brevidecurrens, in 0.4-0.5 decurrentia antici basis, acute convoluta faciens angustam tubiformam colpam edentatam vel 1-2 parvis dentibus; margines foliorum aliter saepe integrae. Typus: North of Escatawpa, Mississippi (*Schuster* 27759); in herb auct.

Plants in large but loose mats, near the bases of tree trunks, dull green to olive-green, dull-textured when dry, with strong differentiation into creeping rhizomatous shoot system and ascending, arched, leafy stems. Mature aerial shoots subsimple or rarely pseudodichotomous, usually 3.2-3.8 mm wide; stems rigid, brownish, 180-200 μ in diameter. Rhizoids absent, or virtually absent, on aerial shoots. Leaves

strongly imbricate, when dry somewhat postically secund, when moist nearly horizontally spreading, at an angle of 65-85° with stem (the antical margin at an angle of (45) 55-75° with stem; postical margin at an angle of 85-100°); *leaves slender, narrowly, obliquely, ovate to ovate-falcate to lanceolate-falcate,* varying from 1580 μ long x 840 μ wide to 1800-1875 μ long x 900-1000 μ wide, occasionally to 2000 μ long x 900 μ wide (*length averaging* 2.0-2.2 × *the maximal subbasal width*); insertion of leaf unequally U-shaped, the antical insertion ranging from 525-750 μ (0.6-0.8 *the subbasal width*), the leaf thus *antically relatively short-decurrent; postical insertion relatively short-decurrent,* ranging from 225-320 μ (*ca.* 0.4-0.48 the length of decurrence of the antical portion). Ventral margin of leaf moderately ampliate above the short-decurrent base, the margin (from ampliate region) to the apex averaging almost straight and at right angles to stem; margin, from ampliate area to (and including) the decurrent base, *sharply convolute and reflexed to form a well-defined tubular, basal fold;* postical basal folds of the leaves juxtaposed on the stem, *the stem in postical aspect essentially hidden. Leaf-margins subentire,* the narrowly tapering apex usually weakly bidentate (rarely tridentate), but sometimes ending in a single acute tooth; *postical margin, above base, entire to sinuous,* rarely 1-dentate; *convolute basal margin of leaf with often* 1(2) *spinose but small teeth.* Apical and subapical cells *ca.* 18-20 x 23-27 μ, with large, ± bulging trigones; the marginal cells equally collenchymatous, not thick-walled; median cells similar in size, with similar development of collenchyma, occasionally to 18-23 x 27-32 μ; basal median cells 21-23 μ x 28-38 (42) μ, strongly collenchymatous, with bulging trigones (and occasional intermediate thickenings); cells at base of decurrent strip little elongated, similar to cells of median base, similarly collenchymatous, *ca.* (16) 20-21 x 24-33 μ; oil-bodies segmented. Underleaves small, constantly present, formed of 2-several extremely elongate, slender, largely uniseriate cilia, *without any extensive lamellate development. Asexual reproduction freely present,* by means of propagula from the postical leaf surface. Sex organs unknown.

Type.—On bark of *Nyssa sylvatica biflora,* swampy woods 2-3 mi. N. of Escatawpa, Jackson Co., Mississippi (*Schuster* 27759, April 4, 1953). Known only from the type collection.

Ecology.—On bark, on the fluting bases of swamp tupelo, in a semi-evergreen swamp forest (*Taxodium, Cyrilla, Cliftonia, Leucothöe,* etc.). Annual flooding to a height of 2-3 feet, during the spring, with a dry summer and fall period is typical of the site. Associated herbs on the bases of the trees include *Epidendrum conopseum* (at its northern edge in the Gulf Coast) and *Polypodium polypodioides michauxiana.* The reddish-tinged lichen, *Chiodecton sanguineum,* the hepatics *Mastigolejeunea auriculata, Cheilolejeunea rigidula* and *clausa,* and the mosses *Tortella humilis, Leucodon julaceus, Schwetzkeopsis denticulata* were associated.

Differentiation.—*P. miradorensis* var. *convoluta* differs from the typical species in several salient respects: (a) the postical leaf-base is relatively short-decurrent, the decurrent strip extending down for usually less than 0.5 the merophyte length; (b) this postical basal area is sharply, but quite narrowly reflexed, with the reflexed margin usually edentate, more occasionally bearing a single tooth; (c) the antical leaf-margin is unusually short decurrent, compared to the typical plant (and compared to the "normal" members of the Crispatae). These differences initially seemed so impressive that the writer regarded these plants as possibly specifically distinct. Subsequent study of long series of specimens of *P. miradorensis* has demonstrated that the latter frequently produced phases with virtually edentate leaves, whose postical base may bear only 1-2 teeth. Such plants represent a partial transition to the var. *convoluta.*

Study of a series of plants of the var. *convoluta* has shown that occasional leaves may show a decurrence of up to 0.6 the merophyte length. Such instances show that this plant actually belongs in the Sectio Crispatae. However, the unusually short postical decurrence of most leaves at first glance would suggest that the variety does not belong here, but rather in the Hypnoides. However, *P. miradorensis* var. *convoluta* differs from *P. hypnoides* and its immediate allies in the subentire leaves, the development of a water sac at the postical leaf base, and in the underleaves, which are formed of several linear elongate cilia.

In the narrowly convolute, tubular postical leaf-bases, *P. miradorensis* var. *convoluta* approaches the Mexican *P. schliemiana* Gottsche (as figured in Gottsche, 1863, pl. 1). However, *P. schliemiana* has freely dentate leaf-margins, and a long-decurrent postical leaf-base. This "species" may be a mere form of *P. ludoviciana.* The leaf-form, and particularly the tendency for the formation of 2 sharp apical teeth terminating the narrow leaf-apex, suggest a weak form of the tropical *P. connata* Lindenb. and Gottsche (as figured in Gottsche, 1863, pl. 8). However, this plant does not have a convolute postical leaf-base, and both antical and postical leaf-bases are markedly decurrent.

PLAGIOCHILA UNDATA Sull.

Fig. 71

Plagiochila undata Sull., Musci Alleghaniensis No. 222, 1845.
Plagiochila crispata Gottsche Mex. Leverm. Dansk. Vidensk. Skrift. 6:167, pl. 15, 1863 (new synonym).

Since detailed study of type material of *P. undata* and of the putative type of *P. crispata,* as well as of a long series of specimens, indicates that the latter intergrades in some respects with the former, I have here treated the two as representing mere geographic races of a single polymorphic species.

PLAGIOCHILA UNDATA subsp. UNDATA Sull.

Plagiochila undata Sullivant, Musci Allegh. No. 222, 1845.

Plants robust, usually in dense, extensive tufts or masses, the ascending aerial shoots at maturity 2.5-3.5 mm wide x 2-5 cm long.

Plants green, occasionally olive-green to olive-brown with age, never distinctly brown, dull. Stems 225-275 μ thick, occasionally to 300 μ thick, brownish with age in many cases, simple or occasionally 1-several times dichotomously furcate. Leaves closely imbricate, the line of insertion exceedingly strongly arched, insertion U-shaped, the *dorsal leaf-base exceedingly long-decurrent, the postical leaf-base nearly equally long-decurrent, the stem virtually or quite hidden both in antical and postical aspect* (the postical decurrent strip broad, usually strongly reflexed to form a vestigial, tubular, postical pocket, extending down 0.7-0.9 the length of the ventral merophytes); leaves obliquely, asymmetrically ovate to triangular-ovate, spreading horizontally on each side when moist, suberect and strongly postically secund when dry, at an angle of *ca.* 45-65° with the stem-apex, *ca.* 1.7-2.0 (2.1) mm long x 1.2-1.4 mm wide (the length 1.3-1.5 [1.65] × the width); leaf widest just above base, the postical border above decurrent base strongly dilated and arched, the postical leaf-margin distad of the recurved base usually at an angle of (75) 90-110° with stem-apex, nearly straight, but more or less *strongly crispate and undulate, nearly or quite edentate;* the narrowed leaf-apex narrowly truncate or rounded-truncate, *bearing* 0-3 (4-5) *obscure to small teeth;* antical margin above decurrent strip nearly straight, but evenly convergent to postical margin, the leaf thus more or less evenly narrowed distally, strongly reflexed for from 0.6-0.9 its length, edentate throughout; median base of leaf strongly depressed, the depression extending out as a broad and shallow sulcus for 0.4-0.6 the leaf-length, resulting (with the reflexed antical margin) in a pronounced convex, inflated appearing dorsal fold or cnemis. Cells of leaf-apex *ca.* 18 μ, of leaf-middle 21-23 μ wide x 28-33 μ, thin-walled to slightly thick-walled with large to distinctly bulging trigones; intermediate thickenings absent; basal cells little wider along midline, *ca.* 18-23 x 27-36 μ, somewhat more elongate but not forming a basal vitta, less than twice as long as wide (on an average); oil-bodies of leaf-middle mostly 4-9 per cell, when few per cell ellipsoidal to ovoid and 5 x 7.5-9 μ, when more numerous often nearly spherical and 4-4.5 μ to 4.5 x 6 μ, formed of rather numerous strongly protruding spherules *ca.* 1-1.2 μ in diameter (22-40 in large oil-bodies in face-view), colorless and rather translucent; chloroplasts averaging smaller than oil-bodies, *ca.* 4.5-5 μ long. Underleaves rather small, lanceolate and with 1-2 marginal (usually subbasal) uniseriate cilia, or bifid and ending in ciliary segments, or divided into 2-5 largely uniseriate cilia, polymorphic. *Asexual reproduction usually absent,* exceptionally with propagula.

Male plants with androecia either intercalary on long, leading branches, or basal on each fork of a furcately (terminally) branched leading axis, then geminate; in either case the androecia becoming intercalary, the axes potentially again fertile and often soon producing secondary androecia. Androecia very compact, spicate, the bracts densely imbricate, commonly in 8-12 pairs; bracts smaller and less typically developed near base and apex of androecium, the androecia

thus somewhat narrowed basally and usually markedly narrowed at apex, below the vegetative proliferation; bracts with basal half strongly ventricose, the median portions erect and imbricate, only the distal parts of antical margin and the apex spreading and often reflexed; postical bases of bracts decurrent like leaves, and the postical margins strongly crispate like those of leaves (diagnosis based on a plant from Orizaba, Mexico, *Farlow, 1885,* which agrees perfectly with subsp. *undata*). Female inflorescences terminal on main shoot, *normally with 1-2 innovations.* Bracts *ca.* 2.6 mm long x 1.7 mm wide broadly ovate-triangular, the base closely sheathing perianth, the dorsal reflexed margin sometimes slightly denticulate; *ventral margin and apex with scattered, small teeth;* postical margin and base usually very strongly crispate. Perianth in lateral view wide-mouthed, almost obcampanulate in outline, laterally compressed above and dorsally keeled (but apparently not with keel winged); mouth bilabiate, ciliate to ciliate-dentate.

Type.—Along Savannah R., Ga. (*W. S. Sullivant,* Musci Alleghaniensis, No. 222, 1845).

Distribution.—ILLINOIS: Southern part of state (Drexler, 1936; according to Frye and Clark, 1944). NORTH CAROLINA: Falls of the Yadkin R., Stanley Co. (*Small* 9683!; as *P. ludoviciana* in herb. Yale); Swamp forest, 1.5 mi. E. of Whiteville, Rte. 74-76, Columbus Co. (*Schuster, Blomquist and Bryan* 29981, 30001; 30001b with *P. dubia*); along Eno R., *ca.* 5 mi. NW. of Durham, Durham Co. (*Schuster* 37480, 37482, 37455, 37482, 37480a; *Schuster and Blomquist* 28216a); along New Hope Creek, Orange Co. (*Schuster* 38197; *Blomquist* 7314!); Linville Caverns, S. of Linville, McDowell Co. (*Anderson* 11029!); Silver Mine Creek, near Hot Springs (*M. S. Taylor* 2361!). (Early reports of the species from North Carolina, based on plants from "Salem" [Winston-Salem], leg. *Schweinitz!,* in the "Herbarium of Columbia College" [NYBG] are based on plants of *Plagiochila yokogurensis fragilifolia.*) SOUTH CAROLINA: Ravine of Estatoe Creek, N. Pickens Co. (*Schuster* 37669, 37669a, with *P. ludoviciana;* 37656a, 37677, 37676, with *P. ludoviciana*); gorge of Whitewater R., S. of Lower Falls, *ca.* 3 mi. N. of Jocassee, Oconee Co. (*Schuster* 27830). TENNESSEE: Lake Calderwood, Blount Co., 975 ft. (*Sharp* 397!); Lake Calderwood, Monroe Co., 975 ft. (*Sharp* 3910!; *c. perianth*!); Walker's Valley, Blount Co., 1400 ft. (*Sharp* 34198!; also issued *in* Verdoorn, Hep. Select. et Crit. *Nos.* 389, 479!); Hiwassee Gorge, Polk Co., 1000 ft. (*Sharp* 160!). GEORGIA: Gorge below Tallulah Falls, Rabun Co. (*Schuster* 34366); Toccoa Falls, N. of Toccoa, Stephens Co. (*Schuster* 25089); Toccoa Falls (*Lesquereux, 1850; L. M. Underwood, Apr. 20, 1891* — Underwood and Cook, Hep. Amer. No. 108!); N. face of granite cliff, Clarke Co. (*R. M. Harper, June 27, 1900*); shaded banks of rivers and wet rocks (*Sullivant, Lesquereux,* Hep. Borealis-Americanae, Austin 1873, No. 10!); Magnolia Park, Thomasville (*C. C. Haynes* 2988! p. p., mixed with *P. ludoviciana*); Seventeen Mile Creek, Coffee Co. (*R. M. Harper* 2047, 1448c, 2047a!); Chattahoochee Co. (*Roland M. Harper* 1795a!); Brooks Co., near Okapilco Creek (*Roland M. Harper* 1625a!); Dade Co. (*Carroll,* 1945). FLORIDA: Gainesville (*N. L. T. Nelson* 115!); Rock Park, Apalachicola R., Torreya State Park, Calhoun Co. (*Anderson* 5186!); Citrus, Highlands, Polk and Seminole Cos. (Redfearn, 1952); Alum Bluff, Liberty Co. (*McFarlin,* 1935); material from Sanford, Orange Co. (*Rapp*), Sanford (*S. Rapp* No. 14) det. Evans = *P. miradorensis.*

The McFarlin and Redfearn reports need verification. ALABAMA: (*F. E. Lloyd, F. S. Earle, Sept. 1900!*); Tuscaloosa, Tuscaloosa Co. (*Pollard and Maxon* 316!; as *P. ludoviciana* in herb. Yale; a green, slightly shiny mod. *viridis-leptoderma*, with the leaves virtually edentate and the postical leaf-margins with weaker than usual undulations). MISSISSIPPI: Among *P. ludoviciana* (*Schuster* 26796a) on bark of Beech, Wyatt Hills, NE. of Ramsey Springs, W. George Co. (*Schuster* 26796). LOUISIANA: Chinchuba (*A. B. Langlois, April 20, 1891!*); Fricke's Cave, Folsom, bases of trees (*Mackaness*, Mar. *9, 1941!*). ARKANSAS: Sandstone, 8 mi. NW of Boxley, Newton Co. (*Anderson* 12123!); "Lost Valley," 2 mi. NE. of Boxley, alt. 1000 ft. (*Iltis and Moore* 4197); Camp Albert Pike, Little Missouri R., N. of Langley, Ouachita Mts., Montgomery Co. (*Anderson* 11381a!, 11378!).

The report of *P. undata* from Illinois (Frye and Clark, *loc. cit.*) should be verified. On phytogeographic grounds it appears improbable that the species should occur in Illinois.

Variation.—The subspecies is relatively stenotypic, compared to *P. ludoviciana*, but appears to show a considerable amount of variation in two chief directions: (1) Development of marginal teeth. Typically, the rounded to subtruncate leaf-apex bears no teeth, or occasionally 1-3, rarely 4 minute, obscure denticulations (Fig. 71:1, 3). Occasionally the apical teeth are 4-5 in number (Fig. 71:4), as in the material from St. Martinsville, La., at Chinchuba (*Langlois*, 1891, NYBG), and then the postical margin may show traces of a few. Similarly, material from Florida (figured by Kurz and Little, 1933) shows 3-5 apical, rather discrete teeth. Such plants, with evident denticulation, represent intergradations to *P. u. crispata*. (2) Degree of development of the undulation of the leaf. Typically, the subspecies *undata* shows a few, broad, relatively salient undulations of the postical leaf-margin, while the base may be undulate-reflexed. Occasionally the undulations are less marked individually, but more numerous (again showing intergradation to *P. u. crispata*).

The dentition of the leaves appears to be most marked in small, xeromorphic phases. For example, a collection from Orange County, North Carolina (*Blomquist* 7314, p.p., among *Radula andicola*), of small, brownish-olive plants only 2.2-2.6 mm wide, has the leaves with strongly developed teeth. Most leaves bear 3-5 sharp teeth apically, some of which are 2-3 cells wide x 3-5 cells long, rarely attaining a length of 5-7 cells. Such leaves are more or less repand-crenate to repand-undulate along the strongly crispate-undulate postical margin and base, and occasionally bear well-marked teeth along the postical margin. Even more critical are the plants from the Falls of the Yadkin River, North Carolina (*Small* 9683; Yale; determined by Evans as *P. ludoviciana* evidently on the basis of the strong dentition), in which the leaves are rather atypically drawn out and longer than normal, and in which the dentition is even more strongly marked. In these plants the leaf-apices together with the subapical regions may bear 6-7 sharp teeth 2-4 cells long and 2-4 cells wide at base; the strongly crispate postical margins are also provided with conspicuous, if not very large teeth. The dentition of the leaves is much more marked than in the

Mexican plants of *P. crispata* illustrated in Gottsche (*loc. cit.*, pl. 15), although the female bracts are no more strongly toothed than the leaves. This suggests that the dentition of the leaves does not warrant separation of *P. crispata,* and that any separation, if attempted, must be on the basis of the much more conspicuous dentition of the female bracts. The Small collection is also deviant in that the decurrent postical leaf-bases are conspicuously tubularly reflexed, with the apices of the tubular portion normally marked by a sharp tooth on mature leaves. In both the dentition and sharply reflexed postical bases these plants closely approach *P. miradorensis* from which they are immediately separable on the basis of the strongly crispate leaves.

Perianths are rather frequently developed in this species, although rarely well developed. They often are situated in the fork of a dichotomy, *i.e.*, surpassed by two strong, equal subfloral innovations. Juvenile perianths often are strongly bilabiate, with both antical and postical keels obscurely developed. Each "lip" typically bears 25-30 unequal sharp teeth. By contrast, propagula are rarely developed. I have seen only one collection with them present in any numbers (Orange County, North Carolina, *Schuster and Blomquist* 28197), in which they were strictly limited to the postical leaf faces; a few occur in *Small* 9683. Evidently a much stronger stimulus is needed for propagulum-development in this species than in the allied *P. ludoviciana* and *P. miradorensis,* since when *P. undata* occcurs with the former it is normally propagulum-free while the *P. ludoviciana* is abundantly propaguliferous.

Ecology.—This robust species occurs chiefly in the Piedmont and in the escarpment region, between the Piedmont and Appalachian Highlands, where it may be abundant (particularly in shaded, damp gorges); it is less frequent on the Coastal Plain (where it is largely replaced by the related *P. ludoviciana*). Unlike *P. ludoviciana,* the species occurs most commonly, and most luxuriantly, on shaded, dry to barely damp rocks (where it is found, as at Toccoa Falls, most often with *Porella pinnata, Radula obconica, Leucolejeunea clypeata*). Under the latter conditions, the *Radula* and *Leucolejeunea* are often pioneer, under drier conditions, while *Metzgeria conjugata* is pioneer under moister conditions, and the *Plagiochila* comes in secondarily, after a thin layer of humus has accumulated; at other times, the *Plagiochila* and *Porella* appear to be pioneer. With the development of thick, pure tufts of *P. undata,* soil accumulates, and the *P. undata* mats often serve as a matrix in which ferns (particularly *Asplenium trichomanis;* under very dry conditions sometimes *Polypodium polypodioides*) undergo ecesis.

On dry rocks the species often occurs on both the vertical and weakly sloping faces, sometimes in partial sun. It is then often associated with such xerophilous mosses as *Hedwigia ciliata* and *Grimmia* spp., and with various pioneer lichens.

In the writer's experience, the rock populations of the *Plagiochila* usually serve as a reservoir population for invasion of nearby tree-bases, on which we occasionally find the species (much as is usually the case with *P. ludoviciana*). At Toccoa Falls, for instance, the bark

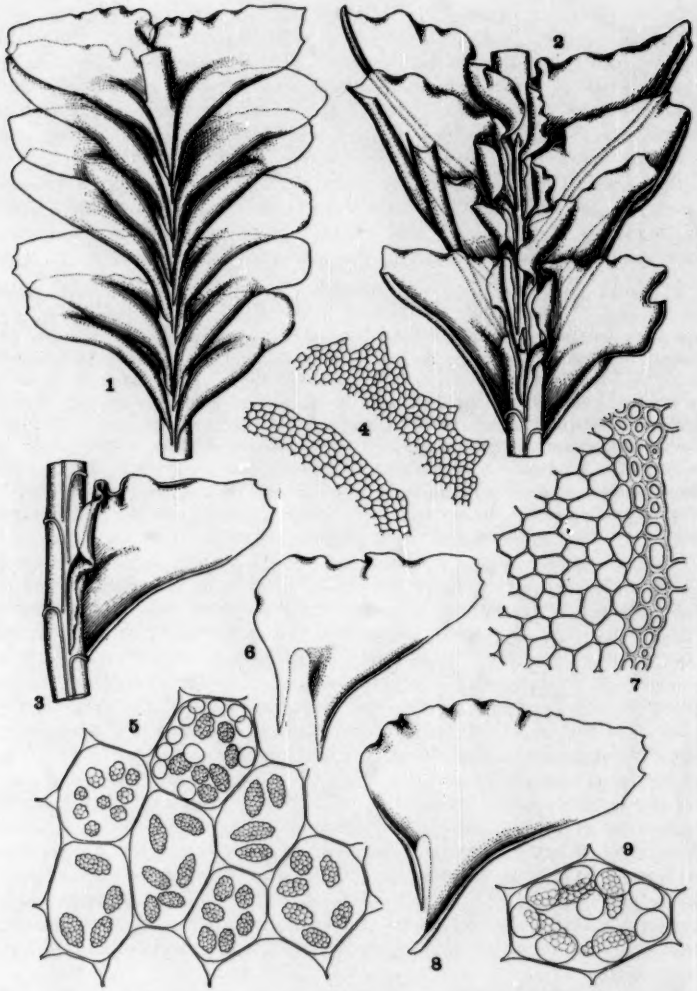

Fig. 71.—*Plagiochila undata* Sulliv. 1. Shoot-sector, antical aspect (x *ca.* 16); 2. Same, postical aspect (x *ca.* 16); 3. Leaf, *in situ*, showing lines of insertion of leaves (x *ca.* 20); 4. Apices of two leaves, showing variation in dentition (x 64); 5. Median cells with oil-bodies (x 500); 6. Leaf (x *ca.* 20); 7. Part of stem cross-section (x 150); 8. Leaf (x 27); 9. Median cells with oil-bodies (x 935). (Figs. 1-3 drawn from type specimen; fig. 5, Toccoa Falls, Ga., *Schuster;* 6, Chunchulla, St. Martinsville, La., *Langlois;* 4. North Carolina, *Schuster* 28197; 7-9, Wyatt Hills, Mississippi, *Schuster* 26796.)

of beeches is often invaded, near the base of the trunk by mosses, *Frullania squarrosa, Polypodium polypodioides, Leucolejeunea clypeata,* and by the *Plagiochila.* When growing on bark, the *Plagiochila* is almost invariably less well-developed than when growing on rocks.

The widespread occurrence of the species (and its occurrence as Massen-vegetation, as at Toccoa Falls), is somewhat inexplicable in view of the fact that prolonged search has not revealed the presence of any common mode of either asexual or sexual reproduction. In the apparently nearly total lack of propagula of the leaf-surface we find an excellent means of separating the species from the related *P. ludoviciana.*

Differentiation.—This large and handsome species can scarcely be confused with any other regional *Plagiochila.* The leaves are very usually subentire, or merely obscurely 2-3 (4-5) toothed apically. On this account, and because of the large size, the species may be confused by the beginner with *P. asplenioides* and its relatives. However, *P. undata* at once differs from these in the undulate to undulate-crispate postical margin of the leaf, with the base strongly reflexed, and often crispate and exceedingly long-decurrent. The leaves are characteristically closely imbricate, and consequently the long-decurrent antical, strongly convex basal "folds" of the leaf are usually so strongly approximated that neither postical nor dorsal stem surface is evident (Fig. 71:1-2).

The species is evidently allied most closely to *P. ludoviciana,* with which it shares an exceptionally long-decurrent postical leaf-base (on normal, well-developed plants the arched, decurrent line of insertion running down the stem nearly to the arched portion of the line of insertion of the leaf below it); reflexed postical leaf-bases; ovate-triangular leaves that are widest near base and long-decurrent dorsally; noncaducous leaves, etc. But *P. ludoviciana* differs at once from *P. undata* in: (1) the more or less spinous-dentate postical leaf-margin distad of the reflexed base; (2) the more or less strongly spinous-dentate distal portion of the leaf; (3) the noncrispate and nonundulate postical leaf-margin; (4) the general abundance of "brood-branchlets" on the lower leaf surface.

The absence of strong and obvious dentition of the leaves, as well as the long-decurrent postical leaf-base, serves at once to separate the species from the rest of our *Plagiochila* species.

The closest relative of *P. undata* is undoubtedly *P. crispata* Gottsche (Mex. Levermosser 71, pl. 15, 1863), and Evans (1896, p. 193) refers the latter, with some doubt, to *P. undata* as a synonym. Evans correctly points out that the differences between *P. undata* and *ludoviciana* are differences of degree, rather than kind. Typically, *P. crispata* has the postical leaf-margin more strongly and regularly crispate-undulate, than in *P. undata,* the plants showing in postical view a leaf-form and orientation that is even more involved and complex than in the regional forms of *P. undata.* However, in addition to the greater degree of wavyness of the anterior leaf-margin, *P. crispata* typically also shows a stronger development of the teeth of the leaf-margins. In our local *P. undata,* the leaf-margins are usually suben-

tire, the subtruncate apex occasionally showing poorly developed traces of teeth. By contrast, a "typical" specimen of *P. crispata* from "Mexico, 3000-8000, Fr. V. Müller" (NYBG, ex herb. Wm. Mitten) shows leaf-margins where the apex bears 3-4 small teeth; the distal part of the antical margin often bears 1-2 teeth, and the postical, crispate margin may bear 2-3 or more teeth (often difficult to demonstrate unless the leaf is flattened out). Stephani (Spec. Hep. II:323, 1903) also emphasizes this difference for the floral leaves stating: *"Plagiochila crispata* G. differt foliis floralibus grosse remoteque spinosis et perianthi ore valide et longe spinosa mecon foliis caulinis apice distincte denticulatis." In *P. undata* the perianth is *ca.* 2 mm long x 2 mm wide, flattened, but campanulate in outline, somewhat bilabiate, with the lips merely ciliate, not spinose-ciliate. The bracts are similar to the leaves, but have the deflexed antical margin "denticulate, postical margin and apex irregularly dentate" (Evans, 1896).

It is therefore evident that *P. crispata* has a strong tendency to develop marginal teeth of the leaves, with the bracts and perianth-mouth becoming spinose; by contrast, the leaves of *P. undata* are typically subentire, while the bracts become denticulate to dentate, and the perianth-mouth merely ciliate. As is evident, these differences, too, are merely of "degree, and not of kind." In addition, I have studied specimens with strongly crispate leaves, which bear more obscure teeth (3-6 per leaf with 1-2 on many of the crispate postical margins), such as a specimen of *"P. crispata"* from Orizaba, Mexico, 1885 (W. G. Farlow), in herb. Yale and NYBG, which evidently bridges the gap between the *crispata* extreme and *undata* extreme. For that reason, it seems that *crispata* represents merely a southern, regional manifestation of what the writer would regard as a more broadly conceived *P. undata*. Under these conditions, it seems reasonable to propose a new combination:

Plagiochila undata subsp. **crispata** (Gottsche) new comb.

Plagiochila crispata Gottsche, Mex. Levermosser 71, pl. 15, 1863.

Specimens examined.—Mexico, 3000-8000 ft., Fr. V. Müller.

In addition to the above specimen of the subspecies *crispata* that I have studied, I have also seen a specimen from Panama (labelled *"crispula"* on the packet), in the Mitten Collection (NYBG). This specimen, very fragmentary, clearly belongs to *P. undata,* but differs somewhat from both *P. undata* subsp. *undata* and the subsp. *crispata* in having the postical leaf-base, just above the decurrent portion, exceedingly strongly dilated. The dilated base is also usually not reflexed, but more generally lies flat or stands slightly away from the postical stem-surface. As a consequence, the postical stem-surface is completely hidden, and the dilated postical leaf-bases may be quite strongly imbricate. This form, in the writer's opinion, should possibly also be recognized as a discrete race. I have also seen another specimen from Panama (Wm. Seeman), in the NYBG, labelled *"Plagiochila crispula* Lindb."; this is filed with *P. crispata* Gottsche. The specimen appears quite inseparable from *P. ludoviciana* Sulliv.

P. undata (in the broad sense) is related clearly to several tropical species, among them *P. crispata-decurrens* (Herzog, 1932, p. 214). The latter shows an even greater development of the decurrent postical leaf-base, which is crisped rather than reflexed to form a water-sac, and has an excessively long-decurrent antical leaf-base. This species also shows large underleaves that are profoundly bilobed and more or less dentate at the bases of the lobes. Some relationship of *P. undata* also exists with the South African *P. crispato-caudata* G., although this relationship is more diffuse.

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A Preliminary Analysis of Habitat Orientation in Microtus and Peromyscus[1]

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Introduction

Each species of organism is restricted in distribution by the limits of its tolerances to the physical and biological factors of its geographical range. In addition, each species is seldom found everywhere within the limits fixed by these tolerances, but appears to be further restricted to certain microhabitats within its environment. This paper is concerned with the orientation of the white-footed mouse, *Peromyscus leucopus noveboracensis* (Fisher), and the meadow mouse, *Microtus p. pennsylvanicus* (Ord), to microhabitats in stages of old field succession on the Piedmont of New Jersey.

This secondary succession proceeds from previously cultivated land through several seral stages. The earliest stages are dominated by annual herbs, chiefly *Ambrosia* and *Oenothera*, but they also contain the subsequent herbaceous dominants in small numbers. By the fifth year several species of *Solidago* and *Aster* have become dominant and generally remain prominent for another 15 years. Broomsedge, *Andropogon scoparius*, reaches dominance by the fifteenth year and remains so for about 45 years. The red cedar, *Juniperus virginiana*, seeds early in the succession and remains the dominant arborescent species for over 60 years. The cedars are joined by the dominant species of a mature oak-hickory forest by the fifteenth year. These oaks are well established in the understory by the sixtieth year, and later constitute the climax forest in this region. *Myrica pensylvanica* and *Rubus flagellaris* are the dominant shrubs in the fields until the twentieth or thirtieth year, when *Rhus radicans* becomes prevalent and remains so to the oldest fields observed.

A series of fields in Franklin Township, Somerset County, New Jersey, represents all the seral stages in this succession. These fields are found on soils of the Norton series formed over the Brunswick formation of the Triassic shales comprising a part of the Piedmont Plateau. A study by Bard (1952) determined the major changes in vegetation occurring throughout the succession discussed above. The results of this study provide an accurate description of the plant variation and the habitat changes.

In 1957 a study of the small mammal populations associated with the secondary succession in these fields provided a foundation for the present project (Pearson, 1959). In addition to indicating the species

[1] This paper is part of a Rutgers Scholar thesis on undergraduate research by the senior author, and directed by the junior author.

present and the relative population levels in the several seral stages, this study established certain patterns of mammal distribution relative to vegetational cover. The results of Pearson's study point out that captures of the white-footed mouse were associated with perennial forbs in the early stages and with shrubs and trees in the late seral stages, and that captures of the meadow mouse and masked shrew, *Sorex c. cinereus* Kerr, were associated with the dense broomsedge cover found in the 7, 11, and 16 year stages.

The present study was conducted in the series of fields studied by Bard (1952) and later by Pearson (1959). The "age" of these fields, as indicated in Bard's study, was the number of years since the land was last cultivated, and the only difference in the habitats used by these three studies was the difference in "age". The "ages" of the fields in this study were 10, 14, 19, and 24 years and each of these was 9 years younger at the time of Bard's study. However, her study included fields approximating the seral stages used in the present study so that reference is still valuable.

This study consisted of four integral parts. The first, running from September 21 to November 7, 1958, was a census to determine the present population levels, to verify the previously determined associations, and to obtain animals for controlled laboratory experiments to be conducted during the winter. The second phase, in the laboratory, was the construction of an artificial habitat in which association could be further tested. The next part was a series of tests to determine the aggressive tendencies of the two species, and the final phase was a release and retrap study carried on from March 8 to March 19, 1959.

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METHODS

Field Study.—Seventy-five traps were set three nights a week during the fall trapping period. Sherman live traps baited with peanut butter were used. Three parallel lines of 8 or 9 traps, approximately 100 feet apart, were placed in each field. Within each line the traps were spaced at approximate intervals of 50 feet. A series of 25 traps remained in a field for the three nights. Traps were run each morning and replenished with bait or dry cotton if disturbed by the weather or a captured animal. During the fall trapping period all of the animals were removed for use in the laboratory. A careful record of the microhabitat immediately surrounding each trap was kept so that the cover most frequently inhabited in these fields by each species could be determined. A record was kept of the date of capture, the sex and species, and the location of capture for each individual. *Peromyscus* and *Microtus* were marked for future identification by the toe-clipping method described by Pearson (1959). All males captured were immediately isolated from each other by an arrangement described later.

During the spring trapping period, in which all animals were released at the point of capture after marking, the traps were set for 10 consecutive nights. They were placed at 50-foot intervals in a grid coverage of the entire field. The traps were again checked early each morning. All the animals held over the winter were released in these fields, and no animals were again removed. Any new individuals captured were marked and immediately released at the point of capture, as were all the recaptures of previously marked individuals.

Habitat Association.—To determine if there was any habitat association exhibited by the two species an artificial habitat measuring four feet on each side was constructed. Its walls were one foot in height and the top was covered with weathered one-half inch hardware mesh. The floor of the whole enclosure was covered with finely sifted sand. This box was divided into two equal compartments with a joining passage. One side simulated the goldenrod-aster habitat and the other the broomsedge. A wooden cubicle approximately one-foot square fit smoothly into the passage, and the animal to be tested was placed within the cubicle. After a one-minute orientation period the cubicle was silently raised, and subsequently removed, allowing the animal unimpeded choice of either simulated habitat, and also free passage between them.

Ordinary drinking straws were used to simulate the upright stems of the goldenrod-aster habitat. They were placed at four-inch intervals in parallel rows four inches apart; the axes of the individual straws being on a diagonal with, rather than perpendicular to, the sides of the enclosure. Additional straws and a small amount of excelsior were scattered on the sand to simulate the litter. Six bunches of excelsior simulated the clumps of *Andropogon,* and a mat of mixed excelsior and straws was spread over the broomsedge habitat to represent the type of cover found in the field.

An opening with a flush door was placed in a corner of each compartment so that the animal, in its natural wanderings along the wall, could wander out of the artificial habitat of its own volition after the timed trial was ended.

The observer sat motionless at one side of the habitat for half of the trials, and moved to the other side for the second half. The lighting was either natural or from a small ceiling bulb in the center of the room. Neither means lighted the habitat directly. The initial choice of habitat, and the time spent in each simulated habitat were recorded for five-minute trials. Notes were kept on the actions of each animal in the habitat during the trial. No animal was tested more than twice in one day.

Aggressive Behavior.—In order to accurately determine the aggressive tendencies of these two species, the males were, as previously mentioned, kept in isolation from the time of capture. No experiments were run for more than a month after capture. Sixteen cages were built into one unit in two rows of eight. The eight pairs were sepa-

rated by sliding aluminum partitions. Two sides of each compartment (each 6″ x 12″ x 8″) were of wood, the third was the metal partition, and the fourth contained a hardware mesh access door, while the top and bottom were of the same wire mesh. Each compartment was provided with cotton nesting material, a water bottle, and a diet of Purina Laboratory Chow, supplemented by fresh fruit and vegetables. Meadow mice were placed in one side and white-footed mice in the other. All females and extra males were retained in large holding cages on the same diet. Only males kept in isolation were used in the aggression studies.

Five-minute trials were run in these experimental cages with no change other than removal of the nesting material. The cage was illuminated by a single shaded bulb suspended six feet above the cages, and the observer again sat silently at one side for half of the experiments and moved to the other side for the second half. The partition was removed and all actions of the two individuals were recorded for the timed period.

Behavior was divided into the following main classifications: 1) actual fighting, 2) aggressive, 3) recessive, 4) fraternal, 5) sniffing, and 6) no conclusive reaction. It was felt that all actions of the animals would fall into one of these six categories. In actual fighting records were kept on which animal initiated the fighting. Squeaking, chasing, scratching and nipping were classified as aggressive behavior. Recessive behavior included wild leaping, clinging to the roof wire, crouching in the corner with eyes closed, or assuming a defensive position similar to that of a human boxer. Also included as recessive was flight from any act of aggression. Mutual grooming or huddling together were considered fraternal behavior. Those actions grouped as no conclusive reaction generally occurred when the animals passed each other, usually going in opposite directions, and there was opportunity for reaction but none appeared. Each of the males was tested with every other male in a round robin fashion, both within the same

TABLE I.—A summary of total trap-nights and captures with regard to habitats in the fall and spring trapping periods

		Trap-nights	*Peromyscus*	*Microtus*	*Blarina*	*Sorex*	*Mus*
FALL	Andropogon	609	14	12	18	4	..
	Solidago-Aster	198	6	1	..	1	..
	Shrubs	155	5	3	..	..	..
	Misc.	88	4	..	3	1	1
	Total	1050	29	16	21	6	1
SPRING	Andropogon	530	19	..	2	..	1
	Solidago-Aster	140	9	..	..	..	..
	Shrubs	30	3	..	..	..	..
	Misc.	50	..	..	..	..	..
	Total	750	31	..	2	..	1

species and with the other species. No individual had more than two encounters in any four-hour period.

RESULTS

Field Study.—The results of 1050 trap-nights covering the fall trapping period are summarized in Table I. All species recorded by Pearson (1959) except *Pitymys* were captured. Computation of the number of trap-nights necessary for the capture of one individual, as taken from Table I, indicates that although the white-footed mouse was captured in all habitats it was most prevalent in the goldenrod. The meadow mouse and the short-tailed shrew, *Blarina b. brevicauda* (Say), were limited in their range, occurring most frequently in the broomsedge habitat. The catches of the house mouse, *Mus musculus* Linnaeus, and the masked shrew were not large enough to be included in the habitat association analyses. The table also reveals that the white-footed mouse was taken more frequently in all habitats than any other species. Moreover, there was a greater number of captures for all species in the broomsedge.

Statistical examination of the above-mentioned associations may be obtained by submitting the trapping data of Table I to a four-fold chi square test of the association between trap-nights of capture and no-capture versus broomsedge and goldenrod habitat. When this was done for *Peromyscus* no significant association was found ($\chi 2=0.1$, $P=0.7$). Similarly no significant habitat association was found in this test for *Microtus* ($1\chi 2=1.2$, $P=0.3$).

The low trapping success of this study made it readily apparent that there had been a significant decrease in small mammal populations as compared to the earlier work of Pearson (1959). This was

TABLE II.—A measure of relative population levels is given where the figures represent average number of individuals caught per census period per 100 trap-nights. The figures in parentheses are for the same fields as reported by Pearson (1959).

	"Age" of field in years			
	10	14	19	24
Total Trap-Nights	225(622)	225(625)	225(597)	375
Peromyscus	0.15(3.2)	0.29(0.2)	1.78(3.3)	1.47
Microtus	0.15(2.8)	0.45(3.7)	..... (5.5)	0.40
Blarina	1.18(0.6)	1.03(1.3)	0.45(1.0)	0.67
Sorex	0.15(0.6)	0.45(1.3)	..... (0.5)	.....
Mus	..... (0.2)	..... (1.6)	0.15(0.1)	.....
All species	1.63(8.2)	2.22(8.0)	2.37(10.5)	2.54

specially true for *Microtus* for they had been quite abundant in the earlier study and considerable effort was expended to get the few males needed for the experimental phase of the present project. However, a comparison of trapping success in the two studies is difficult since a mark-and-release procedure was used earlier for all except *Blarina* while all the animals were removed from the field during the fall in this study. It is seen in Table II that there was little change in the *Blarina* population level from the earlier level.

Even though the indices of population size are not directly comparable for the two studies the data in Table II do show what was also concluded while the field work was underway. That is, there was a significant drop in small mammal population levels. For example, no *Microtus* were taken in the 19-year field where they were most abundant two years before, and their populations were only 60 to 70 percent that of the previous study in the other fields.

It should be noted that the population level, or standing crop of small mammals, increases through the early stages of succession as is apparent from the data in this study, as well as that in Pearson's earlier census.

The results of the spring retrap period, after all laboratory animals had been released, are given in Table I. Three meadow mice were released; they were not retaken and there were no new captures. The white-footed mouse was still the most abundant small mammal and, on the basis of trap effort necessary to catch one individual, it appeared to have a higher population level than in the fall. It was captured with less effort in the goldenrod habitat than in broomsedge. The population level of short-tailed shrews was apparently very low as only two individuals were taken.

Table III.—An analysis of the number of changes made from one simulated habitat to the other; an even number of changes indicates that the animal ended in the habitat of original selection.

Number of changes from original habitat selected	*Peromyscus* Initially Selected: Broomsedge	*Peromyscus* Initially Selected: Goldenrod	*Microtus* Initially Selected: Broomsedge	*Microtus* Initially Selected: Goldenrod
0	9	10	30	3
1	5	5	..	2
2	1	5	5	..
3	2	..	1	1
4	2	1	3	1
5	..	3	..	3
6+	3	2	1	..
Total	22	26	40	10

Habitat Orientation.—Of the 50 artificial habitat trials run, the meadow mice moved initially into the simulated broomsedge habitat in 80 percent of the trials (Table III). They spent 206 minutes in this habitat (82% of the total trial time), and 44 minutes in the simulated goldenrod habitat. In initial habitat selection the white-footed mice showed a random orientation (Table III). They also spent nearly equal time in the two habitats, with 106 minutes in the simulated broomsedge and 133 minutes in the simulated goldenrod.

The data given above and in Table III were tested by chi square to determine whether the observed frequencies of habitat selection and time spent in habitats differed significantly from an hypothesis of random orientation. Analysis of the *Microtus* data indicated significant deviation from random selection on the initial direction of habitat choice ($\chi^2=18$, $P<0.001$) as well as for the total time spent in the two simulated habitats ($\chi^2=105$, $P<0.0001$). Both of these tests verify a positive orientation of *Microtus* to the simulated broomsedge habitat. Analysis of the original choice of habitat and time spent in each for *Peromyscus* gives no evidence of other than random orientation ($\chi^2=0.33$ and 0.23). Thus it appears that there was no positive association between *Peromyscus* and a simulated habitat.

An analysis of subsequent changes in habitat occupancy after the initial movement for the two species is instructive. In 30 of the 40 trials where *Microtus* moved initially into simulated broomsedge the animal remained there for the duration of the five-minute trial (Table III). Also, of the 40 that moved initially into broomsedge only one ended the experiment in the simulated goldenrod habitat. Of the 7 *Microtus* trials where the animal initially chose the goldenrod habitat but later went to the simulated broomsedge, only one returned to goldenrod. There was an average of 1.18 changes of habitat per five minutes for *Microtus*. In contrast there was an average of 2.08 habitat changes per trial for *Peromyscus*. The number of *Peromyscus* remaining in the habitat of initial choice was about equal for both simulated habitats. The number that moved and ended in the habitat opposite to the initial choice was equal also.

During these trials individuals of both species moved chiefly along the walls of the enclosure, particularly on the side simulating the goldenrod-aster habitat. There was movement beneath the excelsior mat in the simulated broomsedge habitat, particularly by the meadow mouse. Animals frequently remained motionless in the corner for long periods in the goldenrod-aster habitat, and there was a tendency for the meadow mouse to remain motionless under the excelsior mat in the broomsedge habitat.

The subjects seldom bolted upon removal of the cubicle, and on occasion remained motionless for as long as two minutes, indicating that the initial response was not motivated by fear. No attempts were made to climb the drinking straws, but the white-footed mice did occasionally climb the enclosure walls and also climbed on top of the excelsior mat in the simulated broomsedge habitat. The animals fre-

quently groomed themselves during the trials, and none of them ate during the trials.

Aggressive Behavior.—Ten intraspecies aggression trials were conducted among the male *Microtus* and 19 among the male *Peromyscus*. The *Microtus* trials resulted in a total of 94 contact reactions, for an average of 4.7 contacts per trial. The *Peromyscus* trials resulted in 190 contact reactions for an average of five contacts per trial. Table IV gives the results of analysis of the contact reactions for both species.

The results of the intraspecies contests indicate that there was little aggressiveness between individuals of the same species. Only a negligible amount of fighting, aggressive, or recessive behavior was exhibited in these intraspecies trials. Dominance between two individuals was established primarily through grooming. The dominant individual groomed, and the recessive individual submitted to the grooming. The pair being tested frequently spent a good part of the period huddled together in a corner.

A total of 108 interspecies aggression tests were conducted, giving 1130 contact reactions, for an average of 5.23 contacts per trial. The average number of contacts per test was about the same for both the intraspecies and the interspecies trials. The analysis of contact reactions for these trials is also reported in Table IV. A comparison of the first three columns for both the intra- and interspecies tests immediately reveals a vast difference in the aggressive behavior of these two species. The figures listed in the first column of Table IV for the interspecies aggression study indicate which species started the fight. The *Microtus* appeared far more aggressive in this respect than the *Peromyscus*. The figures for aggressive behavior substantiate this idea, as does the large percentage of recessive behavior attributed to the *Peromyscus*. No difference for the two species can be noted from the last three columns.

The *Peromyscus* presented an over-all picture of recessiveness. They seldom resisted when the *Microtus* moved into their end of the cage, and removed food or nesting material. Their flight from the advance of a *Microtus* frequently took the form of frantic leaps, or cling-

Table IV.—Tabulation of the results of the aggression studies; figures represent the percent of contacts resulting in the categorized behavior for each species.

	Actual Fighting	Aggressive Behavior	Recessive Behavior	Fraternizing	Sniffing	No Reaction
INTRA						
Microtus	3.19	1.06	2.13	20.22	39.40	34.00
Peromyscus	0.00	0.53	1.05	38.42	21.58	38.42
INTER						
Microtus	79.3	84.6	4.1	45.40	53.20	54.50
Peromyscus	20.7	15.4	95.9	54.60	46.80	45.50

ing to the wire roof of the cage. If they did not flee the meadow mouse's advance they generally assumed the defensive stance, or crouched with eyes closed against the wall. They seldom made any noise in resisting attacks.

Aggressive behavior by the meadow mice was most commonly evidenced by charging and squeaking, directed at the white-footed mice. The meadow mice frequently chased the white-footed mice around the cage, squeaking, and nipping at their hind-quarters. Any assault by the white-footed mice was ignored by the meadow mice. No serious physical injury resulted from any of the fights.

DISCUSSION

The results of the artificial habitat study indicate a positive orientation of the meadow mouse to the broomsedge habitat. Pearson (1959) reports this type of orientation in the natural habitat in the same fields from which these animals were removed. The association has also been noted by Eadie (1953), who suggests that it is a response to the amount of vegetational cover.

The data do not, however, support the position of Pearson (1959) that the white-footed mouse is positively associated with the goldenrod-aster habitat. The fall and spring trapping indicate that the white-footed mouse is captured with less effort in the goldenrod-aster habitat, but in the present study there was no significant statistical association of captures with habitat. The studies in the simulated habitat showed that there may be no differential orientation in selection of habitat and there was no positive association in time spent with either of the habitats.

These artificial habitats were designed to emphasize orientation through visual clues provided by the gross form characteristic of the two microhabitats. However, these were only artificial habitats, and different associations might occur if more emphasis were placed on olfactory or tactile senses. It is difficult to ascertain exactly when and where discrimination actually took place. Perhaps the *Microtus* discriminated at the site of introduction to the habitat, and the simulated broomsedge satisfied the cover requirements of the species. In the orientation trials *Peromyscus* changed habitats twice as much as *Microtus*. This may indicate that *Peromyscus* did not discriminate at the time and point of introduction to the habitat, and/or, neither simulated habitat provided a satisfactory stimulus. Existence of either of the above conditions would produce random search behavior.

The conclusion drawn from the aggression studies is that the meadow mouse is definitely the more aggressive species. Meadow mice were responsible for starting 79 percent of all the fights observed, and they exhibited 85 percent of the recorded aggressive tendencies. The white-footed mice, by comparison, exhibited 96 percent of all recorded recessive activity. The recessivity of white-footed mice has been recorded by King (1957), whose study was on conflicts between house mice and deermice, *Peromyscus maniculatus*. A comparison of his re-

sults with those of the present study strengthens the conclusion that the white-footed mouse exhibited very few aggressive tendencies under these experimental conditions.

A significant decrease in population level is apparent upon comparison of the census data from Pearson (1959) with those of the present study. The levels in all but one case have shown a decrease of at least 40 percent, using Pearson's record of captures opposed to the record of the present study. In most cases where heavy *Microtus* activity had been observed two years earlier the runways were still present but little activity was noted. The runway maze was trapped, using the same traps and type of bait employed by Pearson, but few meadow mice were captured.

Consideration of the possible reasons for the change in population levels gives some clue as to why the association of white-footed mice to the goldenrod-aster habitat did not hold. The cyclic phenomenon of population fluctuation for small mammals has been studied by Hamilton (1940), Davis (1933), Christian (1950), Godfrey (1955), Jameson (1955), and others. *Microtus* have an approximate three- to four-year cycle, and Christian has advanced the theory that adreno-pituitary breakdown, resulting from stresses caused by overpopulation, plays an important role in the sudden increase in mortality. Only three female meadow mice were taken in the census, and two of them, plus six males, died within two months of capture. The deaths observed were accompanied by symptoms similar to those described by Christian of adreno-pituitary breakdown.

On the basis of these observations it appeared that the *Microtus* population in the area studied had recently passed the height of its cycle and had moved rapidly downward.

Pearson (1959) concluded that the white-footed mouse was associated with the goldenrod habitat, while the results of the present study indicate that the white-footed mouse is randomly oriented. The orientation for this species to habitats other than broomsedge which Pearson reported was probably due to: 1) the high level of the *Microtus* population, 2) the positive orientation of *Microtus* to the broomsedge habitat, and 3) the aggressive tendencies of *Microtus* experimentally suggested by this study. The increased number of captures of *Peromyscus* in the broomsedge habitat can probably be attributed to the low *Microtus* population level, and the subsequent lack of sufficient aggressive response by the meadow mouse to the entrance into the broomsedge of a larger number of white-footed mice.

An examination of the broomsedge habitat and the goldenrod-aster habitat reveals a great difference in the type and amount of cover provided. The former, with its dense mat of short grasses, lichens, and young plants, interspersed with large clumps of broomsedge, provides a continuous cover for runways and feeding activity. This may be another reason for the high utilization of the broomsedge habitat reported by the current census. The goldenrod-aster habitat has a low ground cover of annual and perennial herbs, not forming a continuous cover, and an upper layer of the stems and leaves of the forbs. The

broomsedge habitat provides year-round cover while the forb cover is largely destroyed during the winter, beaten down by rain and snow, leaving only underground burrows for shelter.

Additional information on the orientation of these two species will probably be obtained upon further study of their feeding habits. The meadow mouse may be restricted in its habitat association by its utilization of the shoots and leaves of plants. The white-footed mouse appears to feed chiefly upon trees and shrubs. Upon examination of the vegetation of most fields, it is apparent that the production of forbs and grasses is far more regular than the production of mast and fruit. The irregular pattern of tree and shrub growth, as compared to the extensive ground covering in the broomsedge habit makes it possible that the white-footed mouse is, of necessity, more widely oriented with regard to habitat. Hamilton (1937b) gives the meadow mouse a home range the size of a tennis court while Blair (1942) gives the male white-footed mouse a home range of around 2.31 acres. Food preference may, therefore, have an effect upon the habitat orientation in these two species.

SUMMARY

1. Although there was no statistical association between capture of meadow mice and the broomsedge habitat established by the census, the artificial habitat studies indicate that *Microtus* is positively oriented to the broomsedge habitat.

2. The artificial habitat studies indicate that *Peromyscus* is randomly oriented with regard to habitat, and the trapping data reveal that this species was captured in all major habitats. Though it was most prevalent in the goldenrod, there was again no statistical association between capture and goldenrod.

3. Studies of aggressive tendencies point out the fact that the meadow mouse is more aggressive than the white-footed mouse.

4. The occurrence of the white-footed mouse may be affected by the population level of the meadow mouse. The meadow mouse is positively oriented to the broomsedge habitat, it is more aggressive than the white-footed mouse, and when the population level is high for the meadow mouse few white-footed mice are found in the broomsedge habitat.

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The Taxonomic Status of Eleocharis elliptica

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During the course of an investigation of the Cyperaceae of Illinois, great difficulty has been encountered in determining some species of *Eleocharis*. Further study revealed many irregularities which exist in several species complexes. This paper is an attempt to show the relationships believed to exist in one of these complexes in Illinois.

In this study, 157 mature individual plants were examined. The authors wish to thank the curators of the following herbaria who kindly loaned specimens of *Eleocharis:* Chicago Museum of Natural History, Illinois State Museum, University of Illinois, Illinois Natural History Survey, Western Illinois University, and Eastern Illinois University.

Recent Taxonomic Status

The taxonomy of *Eleocharis tenuis, E. elliptica,* and *E. compressa* has been difficult and interpreted differently by various workers in the past. In Illinois, Jones (1950) and Jones, *et al.,* (1955) recognized *E. tenuis* and *E. compressa* while placing *E. elliptica* in synonymy with the former. Gleason (1952) likewise recognized *E. tenuis* and *E. compressa,* but following Svenson's proposal in 1932, relegated *E. elliptica* to varietal status under *E. tenuis,* as var. *borealis.* Fernald (1950) and Svenson (1957), the most recent monographer of the genus, maintain all three species as distinct, although Svenson states that *E. elliptica* and *E. compressa* may tend to intergrade at their range's limit.

Eleocharis tenuis has been divided into three varieties, with only var. *verrucosa* occurring in Illinois. The typical variety from the east coast and var. *pseudoptera* from the eastern states are excluded from this discussion.

The characteristics that are used usually to distinguish *E. tenuis* var. *verrucosa, E. elliptica,* and *E. compressa* follow:

E. tenuis (Willd.) Schultes var. *verrucosa* Svenson.—This taxon is characterized in most treatments as having culms 4- to 5-angled, a mucro at the tip of the truncate sheath, the lowest scale of the spikelet suborbicular, and the achene 0.8-1.0 mm long, olivaceous, warty, with a depressed tubercle ⅛ the length of the achene.

E. elliptica Kunth.—This species is usually described as having culms 6- to 8-angled, a short mucro at the tip of the truncate sheath, the lowest scale of the spikelet suborbicular, the achenes 1.0 mm long, yellow to dull orange, undulate, with a depressed tubercle with an apiculate center.

E. compressa Sull.—This species is traditionally characterized by its strongly flattened culms, its truncate sheath which is faintly to prominently toothed, and its achenes 1.0-1.5 mm long, golden-yellow

to brown, granular-roughened or reticulate, with a depressed or globose-conic tubercle.

ANALYSIS OF CHARACTERS

Culm angles.—In the past one of the best ways given for distinguishing these three taxa is on the shape of the culm. *Eleocharis tenuis* var. *verrucosa* is reported to have a 5-angled (rarely 4-) culm, *E. elliptica* a 6- to 8-angled culm, and *E. compressa* a merely flattened culm. Thorough study of the culms of these taxa shows that these differences are attributable to the number of vascular bundles present in the culms. Thus *E. tenuis* var. *verrucosa* always has 4 or 5 bundles per culm, thereby accounting for the 4- to 5-angled culm. When 5 bundles are present, the culm has a pentagonal shape. (For illustrations, refer to Svenson, 1932.) *E. elliptica* has been described as having culms with 6-8 angles. The angled appearance is due to the presence of 6-8 vascular bundles. (One exception was a non-angled specimen with 6 vascular bundles.) In some instances the angled appearance of culms with 6 to 8 vascular bundles may be due to desiccation from preserving; the tissue opposite the bundles protrudes inward. The angles of these culms are less pronounced than the angles of *E. tenuis* var. *verrucosa*. *E. compressa* has been described as having compressed culms. Those specimens with compressed culms possess 9-14 vascular bundles. In most instances the culms did not appear to be prominently angled due to the more or less bilateral arrangement of the bundles which give the culms a flattened appearance. The width of the culm, correlated with vascular bundles per culm, is tabulated in the following table. Some overlapping of culm width does occur.

Vascular Bundles	Average Culm Width
5	0.3-0.6 mm
6-8	0.4-1.1 mm
9-14	0.9-1.5 mm

Tip of sheath.—All three entities bear truncate sheaths, with short mucros attributed to *E. tenuis* var. *verrucosa* and *E. elliptica*. *E. compressa* is said to have a toothed sheath apex. Our study finds that while mucros are generally present in *E. tenuis* var. *verrucosa* and *E. elliptica*, there are some specimens in which a mucro is lacking. *E. compressa* is usually truncate without a mucro; however, in a few specimens a mucro is present. Because of the spasmodic occurrence of the mucro, little significance can be given to this character.

Lowest sterile scale of spikelet.—The lowest scale of the spikelet in *E. tenuis* var. *verrucosa* and *E. elliptica* is said to be suborbicular. No mention is ever made of the lowest scale in *E. compressa*.

A study of the Illinois material shows that *E. tenuis* var. *verrucosa* and *E. elliptica* always have a lower scale that is suborbicular and completely encircling the culm. Ninety-eight percent of the E. *compressa*

examined have the same type of lower scale. No taxonomic value may be given to this character because of its presence in all three taxa.

Fertile scales.—The fertile scales of Illinois *E. tenuis* var. *verrucosa* are ovate, obtuse or acute, dark purple or black with a light green midrib. The fertile scales of Illinois *E. elliptica* and *E. compressa* are almost identical, both having fertile scales ovate to lanceolate, obtuse to acute, with varying color. The scales of *E. compressa* were usually slightly larger, and the tips of the scales were more commonly bifid in *E. compressa* than in *E. elliptica.*

Achene size.—Achenes range in length (minus the tubercle) from 0.6 mm to 1.2 mm. Specimens with 5 vascular bundles per culm (*E. tenuis* var. *verrucosa*) have slightly smaller achenes. Those with 6-14 vascular bundles per culm (*E. elliptica* and *E. compressa*) have similar sized achenes (0.8-1.2 mm long, 0.6-0.9 mm) wide. On this basis no distinction is possible between *E. elliptica* and *E. compressa.*

Achene color.—Another character usually considered useful in separating the three taxa is achene color. Achenes of *E. tenuis* var. *verrucosa* are said to be olivaceous, *E. elliptica* to be yellow to dull orange, and *E. compressa* to be golden-yellow to brown. By reference to Ridgway (1912), the mature achenes of the Illinois material could be divided into 24 technical colors. Since many of these colors are very close to each other and because such a large number is difficult to work with, the 24 colors were subdivided into four "basic color" groups. These four, along with their included technical colors, are as follows:

Orange Brown—Mars Yellow, Raw Sienna, Tawny.

Yellow—Empire Yellow, Light Cadmium, Aniline Yellow, Yellow Ocher, Olive Yellow, Cream Buff, Reed Yellow, Honey Yellow.

Olive—Sulphine Yellow, Ecru Olive, Light Yellowish Olive, Yellowish Olive, Dark Greenish Olive.

Brown—Ochraceous Tawny, Buckthorn Brown, Dresden Brown, Mummy Brown, Old Gold, Isabella Color, Tawny Olive, Saccardo's Umber.

The achene color is exceedingly variable. Many specimens have two or sometimes three basic color types of achenes. Of the four basic groups of color, yellow is present in all three taxa. Brown is common in specimens usually referred to *E. elliptica* and *E. compressa* while it is almost completely lacking in *E. tenuis* var. *verrucosa.* Olive is found almost exclusively in those specimens called *E. tenuis* var. *verrucosa.* Aside from the normal yellow color sometimes found in *E. tenuis* var. *verrucosa,* a dull yellow color could be induced on some of the mature olive achenes by scraping off the outermost cell wall layer. Orange brown is common in *E. compressa,* occasional in *E. elliptica,* and completely absent in *E. tenuis* var. *verrucosa.* In most instances color may

be used to segregate most specimens of *E. tenuis* var. *verrucosa* from specimens of *E. elliptica* and *E. compressa,* but color cannot be used to segregate *E. elliptica* from *E. compressa.*

Shape of tubercle.—The study of Illinois material reveals that the tubercles in all three taxa may be conical, depressed, or depressed with an apiculate center. All types may be found occasionally on the same plant.

Size of tubercle.—Width measurements of the tubercle were taken on all specimens that had 6 or more vascular bundles. Specimens with 6-8 bundles have on the average slightly wider tubercles (0.4 mm) than those with 9-14 bundles (0.3 mm wide). The height of the tubercles was variable in both groups.

SUMMARY AND CONCLUSIONS

1. Whether the culm is angled or compressed depends upon the number of vascular bundles present. In general, the three taxa fall into three different groups.

2. The tip of the sheath and the shape of the lowest scale of the spikelet are nearly constant in the three taxa.

3. The fertile scales of *E. tenuis* var. *verrucosa* are generally distinct from the other two taxa, being smaller and darker in color than the scales of *E. elliptica* and *E. compressa.* The scales of *E. compressa* may at times be somewhat larger than those of *E. elliptica.*

4. The achenes of *E. tenuis* var. *verrucosa* are in general smaller than the achenes of the other two taxa. *E. compressa* and *E. elliptica* achenes are about the same size.

5. Color of achenes is exceedingly variable, but olivaceous achenes almost always indicate *E. tenuis* var. *verrucosa.* The other taxa are indistinguishable on achene color.

6. *E. tenuis* var. *verrucosa* nearly always has warty achenes; *E. elliptica* and *E. compressa* are virtually indistinguishable on achene texture; however, many *E. elliptica* achenes may appear to be slightly warty or undulate, whereas all *E. compressa* achenes are reticulate.

7. The shape of the tubercle is too variable among the three taxa to have any taxonomic significance.

8. *E. elliptica* seems to have a slightly wider tubercle than *E. compressa.*

9. It seems best to treat *Eleocharis tenuis* var. *verrucosa* as distinct from *Eleocharis compressa* and to make *E. elliptica* a variety under *E. compressa.* For this latter transfer, the following combination must be made:

Eleocharis compressa Sull. var. **borealis** (Svenson), comb. nov.

Eleocharis elliptica Kunth, Enum. Pl. 2:146. 1837.
Eleocharis capitata var. *borealis* Svenson, Rhodora 34:200. 1932.

A KEY TO THE COMPLEX OF ILLINOIS ELEOCHARIS TENUIS

A. Culm with 5 vascular bundles and appearing 5-angled; mature achene usually olivaceous, warty, 0.6-0.9 mm long (excluding the tubercle) ..... *E. tenuis* var. *verrucosa*

A. Culm with 6-14 vascular bundles and appearing with low angles or compressed; achene usually yellow, brown, or orange-brown, reticulate or slightly warty, 0.8-1.2 mm long (excluding the tubercle).

B. Culm with 6-8 vascular bundles and appearing with 6-8 low angles; achenes slightly warty or reticulate ..... *E. compressa* var. *borealis*

B. Culm with 9-14 vascular bundles and appearing compressed; achenes reticulate ..... *E. compressa* var. *compressa*

ABERRANT INDIVIDUALS

To avoid confusion 3 specimens were not used in the previous study. A brief description of these follows:

Hatcher 147, SIU.—Culms with 4 vascular bundles; achenes 1.1 mm long, 0.7 mm wide, brown, reticulate; tubercle depressed, 0.5 mm wide.

William Hardy 9, SIU.—Culms with 4 vascular bundles; achenes 1.0 mm long, 0.8 mm wide, brown, reticulate; tubercle depressed, 0.5 mm wide.

William Hardy 9, SIU.—Culms with 5 vascular bundles; achenes 1.0 mm long, 0.8 mm wide, brown, reticulate; tubercle depressed, 0.5 mm wide.

The above specimens were collected at the same area on the same date. Unfortunately the whole plants could not be observed as the two herbarium sheets that these specimens were mounted on were composed of loose aggregations of culms.

Hatcher 147 (culm with 4 vascular bundles) was with a specimen that had a culm with 6 vascular bundles, achenes 1.1 mm long, 0.8 mm wide, brown, reticulate, and the tubercle depressed and 0.5 mm wide.

The achenes of the above specimens looked identical, and the various culms of these specimens may actually be from the same plant, thus leading to greater confusion within the group. The significance of these plants is at the present time unknown, thus meriting further investigation.

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The Maintenance of the Sternal Egg Sac Position by Pisaurid Spiders

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Nursery web spiders (Pisauridae) have as their closest known relatives the wolf spiders of the family Lycosidae (Bishop, 1924). Among the differences used to separate these two taxa are the conformation of the egg sac and the manner in which the female spider carries the sac. The pisaurid egg mass is enclosed in a continuous covering of silk and is held beneath the female's sternum by the chelicerae. The lycosid egg sac is composed of two valves. It is attached with webbing and swung below the mother's spinnerets. Gertsch (1949) mentioned that the sternal egg sac position is more ancient and awkward than the abdominal position. The purpose of this paper is to suggest a reason for the maintenance of the sternal egg sac position by pisaurid spiders.

McAlister (1959) pointed out that the ability to dive beneath the water is an escape mechanism important to the survival of *Dolomedes triton sexpunctatus* Hentz. This is probably true for the other species of diving pisaurids. It can be explained that if the ability to dive successfully is an asset to these spiders, then the sternal egg sac position is also advantageous, for it facilitates the diving process more than would the abdominal position.

An adult female *D. t. sexpunctatus* weighing 1.50 gm. (equivalent to 1470 dynes) displaced 1.53 gm (1499 dynes) of water when completely immersed. When this individual is submerged there is a buoyant force of 1499 dynes tending to push her to the surface. The spider must therefore exert a force of 29 dynes upon some support to remain underwater (Fig. 1A). This specimen carried a spherical egg sac 1.6 cm in diameter which had a mass of 2.10 gm (2058 dynes). Assuming the sac to be a perfect sphere, its volume was calculated at 2.15 cc. The buoyant force on the sac will be equivalent to the weight of the water which it displaces (= sac volume) or 2.15 gm (2107 dynes). Figure 1B indicates that a downward force of 49 dynes must be provided by the spider to keep her egg mass from bobbing to the surface. The female spider must overcome a net unbalanced force of 78 dynes to remain submerged with her burden. It is important to note that the larger buoyant force vector, that acting on the egg sac, is directly beneath the spider's body where it can be most easily balanced by the tension force of the ambulatory legs (Fig 1C). If the egg sac were posteriorly located it would tend to raise the hind end of the spider, or at least to unbalance her.

The force which a spider must exert to remain submerged is small compared to that which is required for it to break the surface film. An individual *D. t. sexpunctatus* with a mass of 0.447 gm (438 dynes)

fell through the surface film of water when the surface tension was reduced to 38.8 dynes/cm. These figures can be substituted into the formula $St = \frac{Wt^*}{2L}$ to compute the effective contact line between the animal and the surface film (in this case 11.3 cm). This contact line computation can be used as a constant, if the same individual

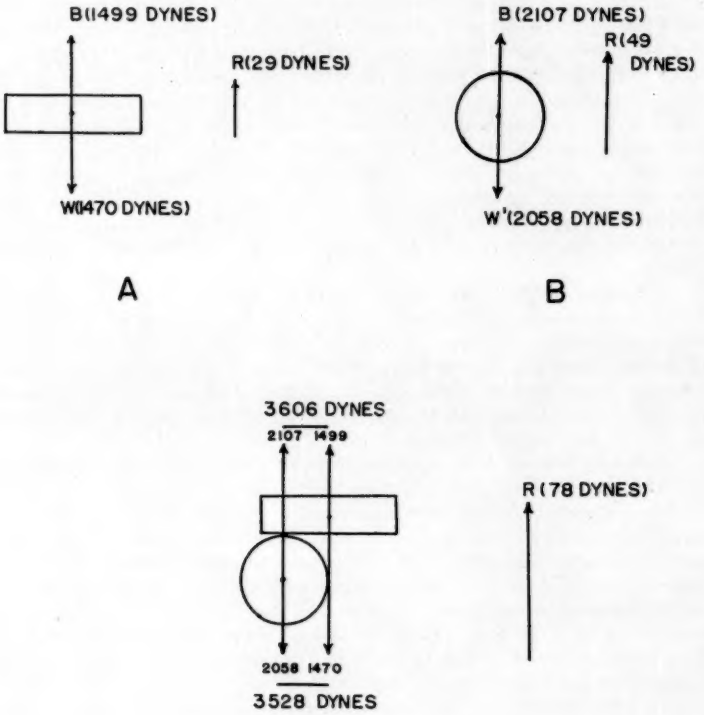

Fig. 1.—Diagrammatic representation of force vectors involved in the diving and submersed activities of the spider, *D. t. sexpunctatus* (rectangle), with its egg mass (circle). Abbreviations are as follows: B—buoyant force; W—weight of spider; W'—weight of egg sac; R—unbalanced force.

* St is the surface tension in dynes/cm; Wt is the weight of the animal in dynes; 2L is the line of contact between the organism and the surface film, in centimeters.

spider is concerned, to determine that in pond water (St =65 dynes/cm) a force of 735 dynes must be created for this specimen to break the surface film. When the egg sac mentioned above is considered, the known diameter (1.6 cm) can be used to figure the contact line, which will be equivalent to the egg sac circumference ($C = 2\pi r$ = 5.03 cm). In pond water at a surface tension of 65 dynes/cm a force of 327 dynes is required to push the egg sac through the surface film. The spider must therefore provide a momentary force of 1062 dynes (or 1.08 gm) when she breaks the surface film of pond water with her egg sac.

McAlister (1959) stated that *D. t. sexpunctatus* enters and emerges from the water head first. Females of this species were observed to dive in this manner with their egg sacs in the San Marcos River, Hays County, Texas. The sternal egg sac position may be related to the diving behavior in either of two ways: a) if the egg sac was sternally carried before the diving behavior developed, the head first manner of breaking the surface film may have become established because it is easier for the spider to overcome relatively large surface film and buoyant forces if the egg sac is directly beneath the body; b) if the habit of diving was developing while the egg sac was carried beneath the spinnerets the movement of the egg mass to the chelicerae may have occurred because it facilitated the diving process and the maintenance of a submerged position. In the first case the egg sac position is a contributory cause, and in the second case a result of the head-first manner of diving. Since Gertsch (1949) considers that the anterior egg sac position antidated the abdominal position, perhaps the first of the above alternatives is the correct one.

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Innate and Environmental Dispersal of Individual Vertebrates

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Little is known about the rates of dispersal of the young of wild populations of vertebrates, because it is difficult to recover marked individuals after they have dispersed to breed elsewhere. Nevertheless, growing evidence suggests that the observed dispersal patterns may be governed by the laws of heredity as well as being influenced by population pressure.

Dispersal of an individual vertebrate is the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate. The significant role of an individual's dispersal is the greatest distance its genetic characteristics are transmitted, rather than the greatest distance the animal may have migrated or otherwise traveled away from the place where it was conceived, hatched or born. Most, but not all vertebrate animals make some sort of a dispersal movement at about the time they attain puberty, regardless of their actual age. Individuals that make innate dispersals, as defined by the hypothesis advanced herein, are predisposed at birth to disperse beyond the confines of their parental home range. They ignore available and suitable niches and voluntarily disperse into strange and sometimes even unfavorable habitats (Fig. 1). In contrast, environmental dispersal is defined as the movement an animal makes away from its birthplace in response to crowded conditions (mate selection, territoriality, lack of suitable homesites, or parental ejection). Environmental dispersers are assumed to have inherited a homing tendency. Environmental dispersal is a density-dependent factor, whereas innate dispersal is independent of density, but both are presumed to be inherited traits.

Even though the hypothesis that vertebrates are predisposed at birth to make either innate or environmental dispersal movements still needs to be substantiated, it seems worth while and desirable to present this concept at this time as a stimulus to further research on this neglected aspect of population ecology. In the literature there are many statements implying that vertebrates disperse because of population pressure factors, but there are relatively few that support the innate dispersal hypothesis.

Burt (1949) wrote, in regard to rodents and other mammals, "If . . . there is an inherent desire to wander, it most certainly is not developed to the same degree in all individuals of a species." Blair (1953) theorized that the dispersal of rodents may result from either population pressure or "an inherent tendency to disperse, stimulated by physiologic changes as the animal becomes sexually active." Dice

and Howard (1951) provide some support for an innate and an environmental dispersal trait, for they found that dispersal distances of prairie deermice (*Peromyscus maniculatus*) are nonrandom — that apparently there is an innate stimulus which might motivate certain individuals but not others to leave the vicinity of their birthplaces. Johnston (1956) similarly found that salt-marsh song sparrows did not have a random dispersal pattern. As with the deermice, too many birds aggregated close by, too few moved intermediate distance (350 to 650 meters), and too many moved beyond 650 meters. He says that both his data and those of Mrs. Nice (Ohio song sparrow) have dispersal curves that differ from the expected significantly at the one percent level.

In an intensive study of valley quail by Howard and Emlen (1942), the birds were marked individually with colored bands, and practically every bird in three of six coveys studied was readily observed each day from an automobile. In this quail population there was an interchange of a few members between coveys prior to the spring nesting. At this time, additional, unmarked birds appeared from more distant coveys, and some resident birds disappeared. In every case when a strange bird attempted to merge with a new covey, it was repeatedly attacked for about a month, and ostracized by the members of the same sex in the covey. These ostracized birds had not been driven from their original coveys; they left voluntarily, and patiently awaited acceptance into a different covey. At that time of the year the birds were pairing,

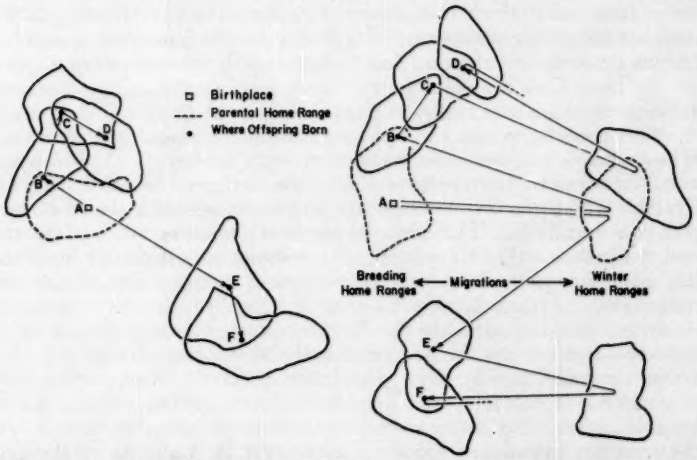

Fig. 1.—A schematic drawing illustrating distance of innate dispersal movements (shortest line between A-E) and of environmental dispersal changes of home ranges (the shortest distance between A-B, B-C, C-D, and E-F) for nonmigratory (left) and migratory (right) animals.

although still in covey formation. Individuals of both sexes made dispersal movements, even though there were unpaired members of the opposite sex in the coveys they left. Perhaps "shuffling" in bobwhite quail is a similar phenomenon and is also composed of innate dispersers.

Von Haartman (1951) made a study in Finland of the tendency of pied flycatchers to return to their birthplaces. According to a review of von Haartman's article by Huntington (1951), about three times as many young females as young males did not return to their birthplaces. Many of these probably made innate dispersals. Of the birds that returned the second and following years after banding, the percentage was about the same for both sexes. Von Haartman considers the homing, or philopatric, quality to be hereditary rather than due to greater success in competition for territory, because combat is unusual in the females, and unsuccessful attempts to settle were much more common in males than in females. Furthermore, the dates of arrival and egg-laying of philopatric females were not significantly earlier than those of others. Apparently the nonphilopatric adult females lack a genetically controlled factor that makes their home-loving sisters try to settle in a familiar place. If that is so, then the nonphilopatric individuals may likewise possess a genetically controlled factor for innate dispersal. Of course, innate dispersal and philopatry may not be the hereditary consequence of each other, but von Haartman does consider the differences, *i.e.*, the variation in dispersal distance, to be inherited. He suggests that philopatry may be a recessive character, because six (3%) offspring of 196 banded philopatric females returned to the area, whereas only three (0.5%) offspring of 632 nonphilopatric females returned. This information is too meager to permit drawing any definite conclusions, but it provides some support for the hypothesis that philopatry, hence, also innate and environmental dispersal, are genetically determined.

There are numerous examples indicating that a certain percentage of both males and females (it will vary with species) is likely to make extensive dispersal movements. Only one case will be cited here. In Fitch's (1948) careful investigation of ground squirrels on an 80-acre plot, he found that 40.9 percent of young females survived to maturity, whereas only 31.1 percent of the males survived. He attributes this difference to an "extensive movement of young males off the area rather than actual mortality."

Introduced animals, like the English sparrow and starling in North America and rabbits in Australia and New Zealand, spread their range far more rapidly than population pressure factors could have demanded. It seems more likely that certain young individuals inherit an instinct to disperse considerable distances, and that is why the range of introduced species is often greatly extended by the time the earlier occupied habitats become crowded.

In 1905, three female and two male muskrats were released in two small natural ponds in Dobrisch, 40 km southwest of Prague.

Nine years later the resulting population in Bohemia was estimated at two million (Mohr, 1933). It takes very little calculation to realize that such a large population could not have resulted if young muskrats had not dispersed until population pressure in each favorable habitat caused them to disperse to the next available homesite. On the contrary, as the result of the presumed innate dispersal urge, there must have been a rapid spreading of individuals into new areas long before the populations they left behind had become very large. By the time the populations in the earlier occupied habitats approached overcrowding, which also probably resulted in increased mortality and decreased fecundity, the range of the species had probably already been extended many miles.

Beer and Meyer (1951) report on muskrats as follows: "The bulk of the reports on movements in the Madison area are received in March with a few in February and quite a few in April. This agrees with the period of increasing gonadotropic activity of the pituitary and the rapid development of the gonads. We believe that these early spring movements may be induced by an increased irritability of the animals or to an urge within the animal to move and that the latter is probably the closest to being correct, since the animals found in the early part of the spring movement have few, if any, wounds from fighting. The group that is found moving from April through July are usually severely wounded from fighting. These movements should be classified as force-out movements induced by population pressures."

Davenport (1915) stated that the nomadic impulse in man is an instinct that is sex-linked. Even though there seems to be little doubt that the dispersal trait is subject to the laws of heredity, additional evidence is necessary before one can be certain that the innate dispersal impulse is sex-linked, sex-modified, recessive, polygenic, or just how it operates.

At the San Joaquin Experimental Range, California, the author captured dispersing rodents in seven funnel traps located along drift fences of hardware cloth (patterned after traps used by Imler, 1945). With the nine species of rodents concerned, results indicate that the dispersal trait might be sex-linked, for about two males were captured for each female. Out of 766 trapped individuals that were carefully sexed, an average of 63 percent were males. It is interesting to note how close all these species independently approached this average. The percentage of male rodents captured between June, 1949, and July, 1952, is as follows (total number of individuals appears in parentheses): *Citellus beecheyi* 71% (7 individuals); *Thomomys bottae* 62% (158); *Perognathus inornatus* 68% (71); *Dipodomys heermanni* 61% (18); *Reithrodontomys megalotis* 63% (65); *Peromyscus maniculatus* 63% (51); *Peromyscus boylei* and *P. truei* 62% (26); and *Microtus californicus* 63% (370). If no locally established rodents or environmental dispersers had been captured, the figure might have been even closer to two males for each female. The traps were examined almost daily for four years and, at that time, it was obvious that nearly all the individuals captured were virgins in the act of dispersing.

In an attempt to measure the degree of dispersal among prairie deermice (*Peromyscus maniculatus*) living on 300 acres of grassland, the birthplace, distance of dispersal, and subsequent breeding site were learned for 155 (77 males and 78 females) of the young deermice (Howard, 1949). An arbitrary figure of 500 feet, which is beyond the boundary of most parental home ranges, is used to separate innate dispersal from environmental dispersal.

The over-all pattern of dispersal observed in the deermice seemed to indicate that: 1) the availability of surplus home sites (at least artificial ones) had little influence on degree of dispersal; 2) virgin mice made their extensive dispersal, if they ever made one, when they attained puberty, regardless of whether at 4.5 weeks or 25 weeks old (reflecting the season when born); 3) even though various proportions of the sexes were found in the same nest during the breeding season (up to two pairs were present together in the same nest boxes), there was no tendency for deermice to aggregate in the presumably more favorable habitats; 4) there was apparently very little trial and error searching for suitable niches, for dispersers were never found at intermediate points, suggesting that the dispersal urge for each individual was satisfied in a day or two; 5) individuals did not make more than one extensive dispersal, even if they later lost their mate, although there were minor shifts of nest sites, usually with each new

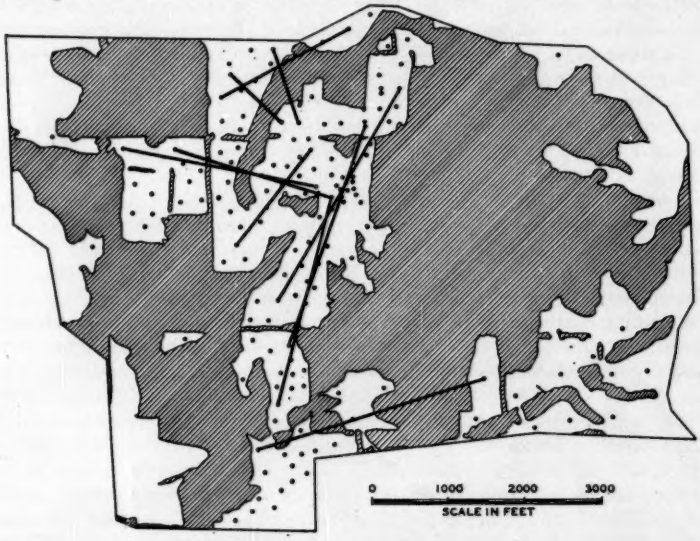

Fig. 2.—The lines indicate ten examples of extensive, innate dispersal movements made by prairie deermice on the Edwin S. George Reserve, Michigan. The grassland areas are unshaded and locations of nest boxes buried in field are marked by dots. (From Howard, 1949.)

litter; 6) when no suitable mates were present, some dispersers remained unmated for several months during the breeding season without moving, and adults did not move whenever an uneven sex ratio developed; and 7) there was no evidence suggesting that the parents forced the young to disperse, for quite frequently the mother would merely abandon the young and seek a new nest when a new litter was due.

With regard to the 36 deermice (out of the 155 that survived to breed) that made "innate" dispersals of 550 to 3300 feet into unfamiliar territory (Fig. 2), the following deductions have been drawn: 1) twenty-four (31%) of the males and 12 (15%) of the females made the extensive dispersals; 2) some individuals traveled through unfavorable habitats (woodland) even though their home range areas were largely surrounded by favorable grasslands; 3) only one animal (a male) was known to return to its birthplace a short time after dispersing (2050 feet); and 4) mice that dispersed the greatest distance did not have time to explore the areas adjacent to their birthplaces or the availability of the habitats through which they passed.

DISCUSSION

If we assume that an innate dispersal trait exists, we can speculate on how the trait may be of value to a species: 1) it would bring about wide outbreeding; 2) it would help reduce the likelihood of too close inbreeding; 3) it would further the spread of new genes; 4) it would rapidly extend the range of the species as favorable habitats become available; 5) it would enable a species to reinvade areas depopulated by catastrophes, such as disease, fire, flood, abnormal weather, or man's activities, without having to start repopulating just at the edges and gradually overflow inward; 6) it would tend to reduce intraspecific conflict and bring about a more efficient utilization of habitat resources; and 7) it might spread a reservoir of characters of possible future value (not adaptive in the new situation yet not selected against, which might help explain why closely related species often differ by characters that are not adaptive).

Domestication probably favors the "homing" or environmental dispersal trait. If such is the case, domesticated animals introduced and released in foreign lands should spread their range more slowly than would be the case with their undomesticated relatives. There is some evidence that this is what happened with many of the introductions in New Zealand and with rabbits in Australia. Perhaps "wildness" is related to the adolescent wanderlust resulting from inheritance of the innate dispersal trait.

For the well-being of migratory species it is not only necessary that some individuals make extensive innate dispersal movements, but it is equally important that all other individuals return to the vicinity where raised. What would happen if most individuals of migratory populations did not tend to return to the home range? Chaos would

develop, for every individual would then be expected to return to the more preferred habitats in the breeding range of the species. There would be so much time and energy spent in establishing individual breeding territories that only a fraction of the total population would be able to breed, if the local food supply were not completely exhausted first. As it is, when the entire breeding range of a migratory bird, fish, or mammal is taken into consideration, there is a far more orderly establishment of the individual breeding ranges and territories than could possibly happen by chance, and natural selection has probably been important in the evolution of this pattern. Territoriality and environmental dispersals are of local importance rather than of geographic significance.

Since such a high proportion of the individuals making up mass emigrations are juveniles (Lack, 1954), it seems highly possible that they may also be responding to the innate dispersal trait. The higher the population density, the greater the number of innate dispersers. Such animals often pass up areas of abundant food supply, and the movements sometimes actually begin before there is any shortage of food. It seems possible that some emigrations, such as an occasional influx of snowy owls into northeastern United States, are merely an increased number of innate dispersers, brought about by an increase in population density rather than by an extensive shift in the home range of older adults. The age of this type of disperser needs to be determined to see if there are any old adults included, *i.e.*, individuals that have bred at least once before making the extensive dispersal. We also need to know if the distance of dispersal is any greater when population density is high.

If animals freely disperse in response to population pressure, then localized epidemics, or "outbreaks," should not occur. On the other hand, even though the direction of dispersal is probably inherently random, the direction of actual dispersal movements are probably greatly modified by many environmental factors. Consequently, there would be a greater tendency—for environmental dispersal movements in particular — toward the more densely populated regions of a species' range, where the more preferred habitats are to be found.

Howell (1922) put many of the factors to be considered in the dispersal of life into chart form. It seems quite plausible that the trigger mechanism initiating dispersals in many vertebrates is associated with the maturing of sex organs, as metabolic processes are speeded up by the activity of reproductive hormones. Lashley (1938) said that the "evidence points to the conclusion that the neural mechanism is already laid down before the action of the hormone, and that the latter is only an activator, increasing the excitability of a mechanism already present." Slonaker (1924 and 1927) recorded the rate of activity of albino rats in a revolving wheel, and noted that there was a marked increase in voluntary activity for males at puberty and for females during each estrus. It would be interesting to see if individuals

possessing the presumed innate dispersal trait had larger adrenals than the environmental dispersers.

Instinctive behavior does not necessarily have to be advantageous to the individual in a social species, but rather it may benefit the group by serving to maintain and spread the species (Tinbergen, 1951: 157). And, as pointed out by Tinbergen, homologous behavior elements may shift their position within the pattern and come to serve different functions in different species, or in some species become lost completely.

Many basic phenomena of animal behavior are not well understood, because they are difficult to investigate. It is particularly hard to analyze the inheritance of behavior patterns. The phenomenon of dispersal alone is a broad subject that will require the participation of many investigators. Much more information is needed about 1) the frequency with which different kinds of animals disperse various distances with population density at different levels; 2) the randomness of the distances of dispersal; 3) the sex ratio of the animals making extensive dispersals in relation to the current sex ratio of the local population; 4) the time relationships of the movements, and whether dispersals are always made at puberty; 5) the motivating and terminating forces, whether physiological or ecological; and 6) the genetic explanations of the variability observed in dispersal distances (field and laboratory experiments). Even if the innate concept should prove to be sound, much information will still be required to learn the various ways in which this behavior is expressed in different animal populations under different situations.

SUMMARY

Dispersal is the movement an organism makes away from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate. For the most part, the major dispersal movements are made by virgins about the time they attain puberty.

Possession of the innate dispersal trait implies that such an animal is predisposed at birth to leave home at puberty and make one dispersal into surroundings beyond the confines of its parental home range. Such density-independent individuals have inherited an urge to leave home voluntarily. They often pass up available and suitable niches and venture into unfavorable habitats.

Animals that make an innate dispersal movement are obsessed with a dispersal instinct. The "purposiveness" of the innate concept is not for the individual's welfare; rather, in spite of the high rate of mortality of innate dispersers, it has distinct survival value for the species. Innate dispersers are particularly important to a species because they, 1) increase the spread of new genes, 2) create wide outbreeding, 3) enable a species to spread its range rapidly as favorable habitats are created, 4) permit the species to have a discontinuous distribution,

and 5) help the species quickly reinvade areas that may have been depopulated by catastrophes, such as floods, fires, or man's activities.

Points that appear more or less to favor the existence of an innate dispersal concept include: 1) the distances of dispersal are, at least sometimes, significantly not random; 2) some introduced species spread their range too rapidly to be the result of population pressure factors; 3) reinvasion of a depopulated area does not commence at the edge and gradually overflow inward, but, instead, the density of the species builds up almost simultaneously over all of the area that is within the maximum limits of innate dispersals; 4) the rate at which innate dispersals are made seems to be density-independent; 5) the movements are made instinctively without any prior experience or instructors to imitate; 6) innate dispersers frequently cross or attempt to cross regions of unfavorable habitat, regardless of the availability of adjacent suitable habitats; and 7) the stimulus is of short duration, apparently being expressed only once, when the animal becomes sexually active for the first time.

The presence of the environmental dispersal trait implies that the individual will remain where born or, by means of trial and error, eventually select a new home range usually within the confines of its parental home range. It will have a strong homing tendency and move only as far as forced by population pressure factors (intraspecific competition or density-dependent factors) such as parental ejection of young, voluntary avoidance of crowded areas, mating and territoriality, availability of food and homesites, or the presence of other organisms including predators. Minor shifts of homesites result in a dispersal, but these are all called environmental dispersals, even though a series of them by one individual might eventually result in a total dispersal distance that is quite extensive, even exceeding that of some innate dispersal movements. Environmental dispersal has only local significance, whereas innate dispersal is of geographic importance.

To verify or refute the existence of an innate dispersal trait, the assistance of other investigators is urgently solicited, for findings of many workers will be necessary before we can thoroughly understand the dispersal behaviorism and dispersal pattern in different species.

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Studies on the Trematode Family Brachycoeliidae III. The Subfamilies Subordinate to the Brachycoeliidae and the Status of the Genus Cymatocarpus Looss, 1899[1]

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In Part I of this series of studies on the trematode family Brachycoeliidae (Cheng, 1958) was given an annotated list of the recognized species of *Brachycoelium* and in the same paper *Brachycoelium* was considered a member of the subfamily Brachycoeliinae under the Dicrocoeliidae; however, in Part II (Cheng, 1959), Brachycoeliinae was elevated to familial rank, following the suggestion of Johnston (1912). The decision to elevate this taxon to familial rank was based on newer information contributed by the discovery of the life cycle of *Brachycoelium obesum* Nicoll, 1914 considered elsewhere. Dispite the elevation of Brachycoeliinae to familial rank, the authors have seen fit to retain Looss' subfamily, Brachycoeliinae, to include the genera *Brachycoelium* and *Cymatocarpus* since these two groups are sufficiently different from the other genera included in the Brachycoeliidae to warrant their being placed in an independent subfamily.

Several other subfamilies have been erected in the past by various workers to receive several of the genera now generally considered to be related to the brachycoeliids. The validity and usefulness of some of these are questionable. Baer (1924) erected Cymatocarpinae to receive *Cymatocarpus;* Dollfus (1937) erected Orchidasmatinae for *Orchidasma,* a genus which cannot be justified as a member of the Brachycoeliidae although it had been considered by some as a close relative of the Brachycoeline Group; Dollfus (1929) erected Mesocoeliinae to receive *Mesocoelium;* and Dayal (1938) erected Leptophallinae for *Leptophallus.* Of these subfamilies, the first two mentioned possess no systematic significance and their deletion is therefore advocated. Cheng (1959) stated that the genera *Glypthelmins, Margeana* and *Reynoldstrema* should be assigned to the Glypthelminae Cheng, 1959, since these three genera are again sufficiently different from the other members of the Brachycoeliidae to warrant their assignment to the same subfamily. In order to clarify what the authors consider a natural systematic classification, the following taxonomic design is proposed and is being used throughout this study.

[1] A contribution from the Department of Biology, Lafayette College and contribution No. 31-C from the Department of Histology and Embryology, Dental School, University of Maryland. This research was made possible by the National Science Foundation Award (Grant-2086) to the senior author, summer, 1958, Mountain Lake Biological Station, University of Virginia.

TAXONOMY OF THE BRACHYCOELIIDAE

Superfamily Dicrocoelioidea Faust, 1929
Family Brachycoeliidae Johnston, 1912
Subfamily Brachycoeliinae Looss, 1899
Genera *Brachycoelium* (Dujardin, 1845) Stiles and Hassall, 1898
Cymatocarpus Braun, 1901
Subfamily Leptophallinae Dayal, 1938
Genus *Leptophallus* Lühe, 1909
Subfamily Glypthelminae Cheng, 1959
Genera *Glypthelmins* Staffod, 1905
Margeana Cort, 1919
Reynoldstrema Cheng, 1959
Subfamily Mesocoeliinae Dollfus, 1929
Genus *Mesocoelium* Odhner, 1911

Cheng (1959) gave the definition of the subfamily Glypthelminae. It is felt that redefinitions of the subfamilies Brachycoeliinae Looss, 1899, Leptophallinae Dayal, 1938 and Mesocoeliinae Dollfus, 1939 are valuable in presenting the phylogenetic relationships within the Brachycoeliidae, hence these are given, incorporating the more recent accumulated information.

Subfamily Brachycoeliinae Looss, 1899

Diagnosis.—With characteristics of the family (Cheng, 1958)[2]; cuticle spinous, more pronounced at anterior end of body; intestinal ceca short, never extending posterior to acetabulum; gonads in middle one-third of body, ovary anterior to testes; vitellaria never extending posterior to level of testes; genital pore between acetabulum and crural fork; excretory vesicle Y-shaped with extremely short cornua.

Type genus.—*Brachycoelium* (Dujardin, 1845); so designated by Looss (1899).

Subfamily Leptophallinae Dayal, 1938

Diagnosis.—With characteristics of family; cuticle completely spinous; intestinal ceca of medium length, reaching through two-thirds of body; ovary anterior to testes; vitellaria limited to exterior one-third of body; genital pore between acetabulum and crural fork; excretory vesicle Y-shaped with extremely short cornua.

Type genus.—*Leptophallus* Lühe, 1909; so designated by Dayal (1938).

Subfamily Mesocoeliinae Dollfus, 1929

Diagnosis.—With characteristics of family; cuticle spinous or aspinous; intestinal ceca of medium length, either limited to anterior

[2] The familial characteristics of Brachycoeliidae given by Cheng (1958: 68) as those of the subfamily Brachycoeliinae which taxon has since been elevated to familial rank.

one-half of body or extending beyond middle of body, never reaching posterior margin of body; testes anterior to ovary; vitellaria lateral to ceca, may intermingle along medial line, never extending to posterior margin of body; excretory vesicle I or Y-shaped.

Type genus.—*Mesocoelium* Odhner, 1911; so designated by Dollfus (1929).

KEY TO THE SUBFAMILIES OF BRACHYCOELIIDAE

1. Ovary anterior to testes.
   - A. Intestinal ceca short, never extending posterior to acetabulum.....Brachycoeliinae Looss, 1899
   - B. Intestinal ceca of medium length, reaching posterior limits of middle one-third of body.....Leptophallinae Dayal, 1938
   - C. Intestinal ceca long, extending short of posterior end of body.....Glypthelminae Cheng, 1959
2. Ovary posterior to testes; intestinal ceca either limited to anterior one-half of body or extending beyond middle of body, never reaching posterior margin of body.....Mesocoeliinae Dollfus, 1929

THE GENUS CYMATOCARPUS

In 1899 Looss established the genus *Cymatocarpus* to receive *C. undulatus,* a parasite of the intestinal tract of *Thalassochelys corticata* from Egypt. This genus was tentatively assigned to the family Dicrocoeliidae although the reasons for this designation was never given. In 1899 Braun described *Distomum soleare* from *Chelone mydas,* and later, in 1901, transferred this species to the genus *Cymatocarpus.*

Linton (1910) identified specimens of *C. undulatus* from the intestines of the loggerhead turtle, *Caretta caretta,* captured at the Marine Laboratory of the Carnegie Institution, Tortugas, Florida. Neither Braun (1899, 1901) nor Linton (1910) attempted to place *Cymatocarpus* in any definite family. A search through the literature revealed that the three above mentioned references are the only existing ones. A careful search for unassigned trematodes which might be considered members of the Brachycoeliidae revealed a startling similarity between *Cymatocarpus* and *Brachycoelium.* The two species of *Cymatocarpus* both possess short intestinal ceca of the type found in the members of *Brachycoelium;* an ovary which is situated anterior to the testes; an anterior sucker and an acetabulum of subequal size, situated in the anterior half of the body; a genital pore which is situated anterior to the acetabulum; ascending and descending uterine limbs; a Y-shaped excretory vesicle; a seminal receptacle, a Mehlis' gland and a Laurer's canal. These characteristics are all common to the species of *Brachycoelium,* in fact, *C. undulatus* and *C. solearis* could almost be considered members of *Brachycoelium* except for the extremely large cirrus pouch which is characteristic of both species. The length of the cirrus pouch in *Cymatocarpus* ranges from 5 to 7 times the diameter of the acetabulum. This peculiar condition is

considered to be of sufficient significance to warrant the recognition of *Cymatocarpus* as an independent genus assigned to the subfamily Brachycoeliinae.

The abbreviated diagnoses of *Cymatocarpus undulatus* and *C. solearis* are given here, as are the original illustrations, to facilitate the identification of the two species.

Cymatocarpus undulatus Looss, 1899

Figure 1

Diagnosis.—Body elongate oval, 2-5.5 mm long, 1-2 mm wide; cuticle spinous; anterior sucker 0.28 by 0.28-0.3 mm, acetabulum 0.24-0.28 mm; prepharynx obscure, pharynx small, 0.09-0.15 mm in diameter, esophagus slender and extremely long; intestinal ceca short, not extending posterior to level of acetabulum; testes irregularly oval, 0.335-0.337 by 0.58-0.67 mm, situated side by side, posterior to acetabulum; cirrus pouch extremely large, approximately 6 to 7 times the diameter of acetabulum in length, containing seminal vesicle and armed cirrus; number of bursae at base of cirrus (4 small and 2 large) lined with fine spines; ovary, 0.2-0.28 by 0.15-0.18 mm, anterior to left testis, posterior to acetabulum; vitellaria lateral, extending from

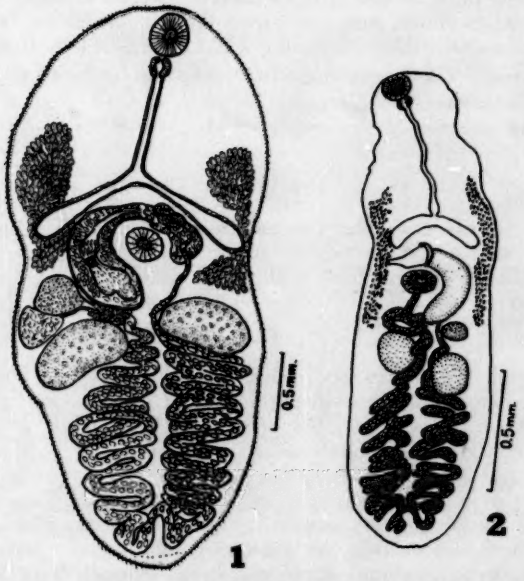

Fig. 1.—*Cymatocarpus undulatus* Looss, 1899. (After Looss, 1899). Dorsal view. 2.—*Cymatocarpus solearis* (Braun, 1899). Dorsal view.

level of midlength of esophagus to beyond cecal tips; ascending and descending limbs of uterus not intercoiled; metraterm with thick glandular wall. Eggs 0.023-0.025 by 0.015 mm.

Type host.—*Thalassochelys corticata.*
Type locality.—Abukir, Egypt.
Type specimen.—Not extant.

Cymatocarpus solearis (Braun, 1899)
Figure 2
Syn. *Distomum soleare* Braun, 1899

Diagnosis.—Body elongate; cuticle aspinous; 2 mm long, 0.6 mm wide; anterior sucker 0.13-0.14 mm in diameter, acetabulum subequal to anterior sucker; prepharynx absent, esophagus long (0.5 mm); intestinal ceca short, not reaching level of acetabulum; testes kidney-shaped, 0.15-0.16 mm in diameter, posterior to acetabulum, slightly oblique, left one slightly anterior to right; ovary 0.07-0.09 mm in diameter, anterior to right testis but posterior to acetabulum; cirrus pouch large, approximately 4 times diameter of acetabulum in length, containing seminal vesicle, unarmed cirrus and prostate glands; no spinous bursae present; vitellaria laterally situated, from level of posterior one-third of length of esophagus to level of anterior margin of left testis; ascending and descending limbs of uterus not intercoiled; metraterm without thick glandular wall. Eggs 0.014 by 0.008 mm.

Type host.—*Chelone mydas.*
Type locality.—New Guinea.
Type specimen.—Not extant.

DISCUSSION

Cymatocarpus undulatus can be distinguished from *C. solearis* by its armed cirrus, spinous bursae at the base of its cirrus, its larger cirrus pouch, its greater body width (1-2 mm wide in *C. undulatus,* 0.6 mm in *C. solearis*), its larger eggs (0.025 by 0.015 mm in *C. undulatus,* 0.014 by 0.008 mm in *C. solearis*), and by its spinous cuticle.

Yamaguti (1958) in his commendable monograph of the digenetic trematodes, also considers the genus *Cymatocarpus,* along with *Brachycoelium,* to be a member of the Brachycoeliinae; however, he does not consider Leptophallinae to be subordinate to the Brachycoeliinae, and since Glypthelminae was not erected until after the publication of his monograph, it was not considered. Yamaguti considers the Leptophallinae a subfamilial group under the Plagiorchiidae, a designation with which the authors cannot agree. Recently Dr. E. H. Cordero (personal communication) stated that the Mesocoeliinae should be considered as an independent family, Mesocoeliidae, however, for reasons which will be presented in a later part

of this series, the authors must consider Mesocoeliinae as a subfamily under the Brachycoeliidae.

No complete life history study is known within the genus *Cymatocarpus*. However, Dollfus (1927) reported the finding of the metacercarial stage of *C. undulatus* encysted in the abdominal muscles of *Pagurus tinctor*. It is not known whether this crab serves as the only or the second intermediate host, and hence until the complete life history is known this information is of little value taxonomically, since it is assumed, from the few life histories known among the members of the Brachycoeliidae, that all of the genera utilize only one intermediate host. It is strongly suspected, however, that *P. tinctor* is the only intermediate host, since in those forms where the life histories are known the metacercaria is found (encysted or unencysted) within the invertebrate host.

KEY TO THE GENERA OF BRACHYCOELIINAE

1. Length of cirrus pouch never greater than twice the diameter of the acetabulum.....*Brachycoelium* (Dujardin, 1845)
2. Length of cirrus pouch 4-7 times the diameter of the acetabulum.....*Cymatocarpus* Looss, 1899

KEY TO THE SPECIES OF CYMATOCARPUS

1. Cirrus unarmed; no spinous bursae present at base of cirrus..... .....*C. solearis* (Braun, 1899)
2. Cirrus armed; spinous bursae at base of cirrus..... .....*C. undulatus* Looss, 1899

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Calamovilfa longifolia and Its Variety magna

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The grass *Calamovilfa longifolia* was described by Hooker (1840) from a collection made in Saskatchewan. Fifty-one years later, Lamson-Scribner and Merrill (1901) recognized a variety of *C. longifolia* that they named *magna,* distinguished from the species "mainly by its large size." In subsequent years this variety has been accepted by some authorities (e.g., Fassett, 1951; Gleason, 1952; Hitchcock, 1935, 1950; and Shinners, 1943) and ignored, overlooked, or not regarded as distinct by others, presumably equally competent (e.g., Deam, 1940; and Fernald, 1950). Those who recognize the variety maintain that it may be distinguished from the species by several characteristics: the greater size of the plant; the greater size of the panicle; the greater spread of the panicle branches; the color of the spikelets; the presence of a tuft of hairs at the summit of the pedicel; the presence of pubescence on the leaf sheaths; and its geographic distribution.

During the summer of 1958 field studies and mass collections of *C. longifolia* were made over much of its range. The analysis of the mass collections and the results of a study of about 1,200 herbarium specimens[1] are the subject of the present paper.

Acknowledgments.—I extend my thanks to Chicago Natural History Museum, whose sponsorship of my 1958 field work made this study possible; to the curators of the various herbaria who made specimens of *Calamovilfa longifolia* available to me; to Chester E. Hansen, faculty member at York Community High School, Elmhurst, Illinois, and my wife, Mildred W. Thieret, who assisted in the onerous task of making the mass collections; and to Samuel H. Grove, Jr., of Chicago Natural History Museum, who drew Figures 1 and 2.

One hundred and twenty-eight mass collections of *C. longifolia* were made in the following states or provinces (see Fig. 1): Alberta (4), Saskatchewan (2), Montana (4), Wyoming (12), North Dakota (1), South Dakota (22), Nebraska (21), Illinois (18), Wisconsin (9), Indiana (3), Michigan (24), and Ontario (8). Each mass collection was from a presumed clone and consisted of two complete culms and usually 12 to 14 inflorescences chosen to represent variation and frequency of variation of size and shape. A total of 1,588 panicles was collected and carefully pressed to retain, as much as possible in two dimensions, natural appearance. For

[1] From these herbaria (abbreviations those of Lanjouw and Stafleu [1956]): ALTA, CAN, COLO, DAO, F, GH, ILL, ILLS, IND, ISC, KSC, MICH, MIN, MO, MONT, NDA, NEB, NY, RM, SASK, SDC, TRT, UBC, UMO, US, WIS, and WS.

specimens collected in the central and northern plains this was no problem because the inflorescences there are for the most part narrow and rather spike-like. The Great Lakes and western Illinois specimens, however, often have panicles so large and spreading that it was sometimes necessary to divide a panicle into two or three sections and press each in a separate sheet. Representative material from each of the mass collections is deposited in the herbarium of Chicago Natural History Museum.

There can be no doubt that variety *magna* is distinct from the typical form of *C. longifolia,* hereafter referred to as variety *longifolia.* Those who question this should observe the grass in the field in, say, the Badlands of South Dakota or the sand hills of Nebraska and then in Indiana Dunes State Park in Indiana or Ipperwash Provincial Park in Ontario. The Great Lakes plant is, to use the words of Shinners (1943), "utterly dissimilar in its appearance in the field." To distinguish the two varieties in the field and on herbarium specimens (almost all of the herbarium specimens I have examined can be placed at a glance into one variety or the other) is one matter, but to record in print the often difficult-to-define differences is quite another.

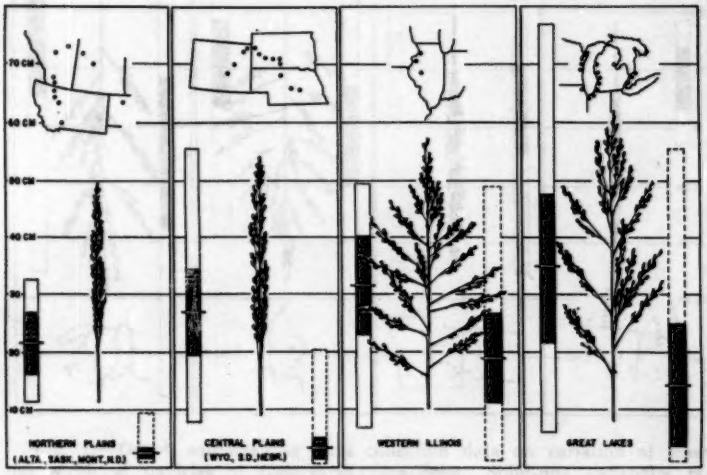

Fig. 1.—Graph summarizing mass collection data on variation of length and width of panicles of *Calamovilfa longifolia.* Solid-line rectangles represent range of length, dotted-line rectangles range of width. Mean figures are represented by cross bars. Shaded areas represent standard deviations from the means. Panicles drawn show "average" specimens. Dots in maps indicate areas where mass collections were made.

Size of the plant.—Culms of var. *magna* average 3 to 4 decimeters taller than those of var. *longifolia.* However, the same maximum height, 23.4 dm, can be reached by culms of each variety. The range of culm height in several presumed clones is as follows:

var. *magna*	var. *longifolia*
11.2 - 16.2 dm	8.6 - 11.2 dm
12.7 - 23.4 dm	9.1 - 11.7 dm
10.7 - 13.2 dm	16.5 - 23.4 dm
6.3 - 12.7 dm	9.9 - 18.3 dm
7.6 - 15.2 dm	6.6 - 10.2 dm
11.2 - 20.8 dm	4.1 - 6.1 dm
19.0 - 21.6 dm	6.1 - 15.2 dm

It is evident from these figures that var. *magna* cannot be distinguished from var. *longifolia* "mainly by its large size," as stated in the original description of *magna.*

Inspection of the data in Table I and of the graph in Figure 1 indicates that, on the average, panicles of var. *magna* are longer by about 9 cm than those of var. *longifolia.* The amount of overlap in panicle length, however, detracts considerably from the usefulness of this character. Panicles are, on the average, considerably wider in *magna* (by about 14 cm) than in *longifolia,* and there is much less overlap in width than in length. A still more useful characteristic to distinguish the varieties is the ratio of panicle length to panicle width (l/w). Panicles of *longifolia* average about 10 times as long as broad, while those of *magna* average only 3 times as long as broad. Panicle branches of *magna* attain greater lengths — up to 33 cm — than those of *longifolia,* which reach as much as 23 cm only rarely. The width of the panicle in either variety depends in part upon the amount of divergence of the branches, a characteristic discussed in the following paragraph.

Spread of the panicle branches.—The amount of divergence of the panicle branches furnishes an excellent characteristic to set apart the varieties. In *longifolia* the panicle branches are usually appressed or strongly ascending (angle of divergence less than 15°). However, panicles of *longifolia* can be found wherein the lowest branches diverge as much as 50°, but even in these panicles the branches in the terminal third of the panicle are appressed or strongly ascending.

TABLE I.—Panicle size (in centimeters) in two varieties of *Calamovilfa*

	magna			*longifolia*		
	Length	width	l/w	Length	width	l/w
mean and standard deviation	33.7± 11.3	16.8± 9.6	3.4± 2.1	24.4± 6.4	3.0± 1.3	10.3± 3.6
maximum	77.5	57.0	16.2	55.5	20.8	36.7
minimum	6.3	0.7	0.9	7.9	0.8	1.6

Panicle branches of *longifolia* are comparatively rigid. In *magna* the often flexuous or lax panicle branches are mostly strongly divergent, commonly exceeding 50° in the lowest third of the panicle, and some branches, especially the basal, may be reflexed.

Color of the spikelets.—The basic color of the spikelets of *longifolia* is a straw yellow that approaches reasonably close to the "cream color" of the Ridgway standard (Ridgway, 1912). It may, however, be slightly lighter or somewhat greenish tinged. A violet-purple, approaching the "dark hyssop violet" of Ridgway, may overlay the basic "cream color," appearing only as a trace on the glumes or becoming more general over the glumes, lemma, and palea, and even spreading to the anthers. When growing side by side, the color extremes — a clone with "cream color" panicles without a trace of anthocyanous pigmentation and a clone with panicles deeply suffused with "dark hyssop violet" — are strikingly distinct and suggest that the color differences are genetically controlled. The amount and intensity of the "dark hyssop violet" appear to be influenced to some extent by exposure to light.

As in *longifolia,* the basic color of the spikelets of *magna* is "cream color," and over this may be laid varying amounts of "dark hyssop violet." However, with or without this "dark hyssop violet" a brownish cast may be laid over the "cream color." When present, as it commonly is in *magna,* this brownish cast is a useful characteristic to distinguish the varieties, giving to panicles of *magna* a different appearance colorwise from those of *longifolia,* which only very rarely have this brownish cast.

Pedicel hairs.—This characteristic is used by Fassett (1950) as follows: var. *longifolia,* "summit of pedicels always glabrous"; var. *magna,* "often with a tuft of hairs at the summit of the pedicel." Unfortunately these distinctions do not hold. Of the 818 panicles of *longifolia* examined by me, 47 percent showed at least a few hairs on the summits of some of the pedicels. Of 770 panicles of *magna,* 58 percent showed pedicel hairs. These hairs occur more frequently in *magna* than in *longifolia* and mostly in greater numbers per pedicel. However, too much overlap in this character renders it of little taxonomic use.

Pubescence of the leaf sheaths.—Each of the 124 culms of *magna* collected by me had at least some pubescence on the leaf sheaths, especially the lower. In contrast, only 12 percent of 132 culms of *longifolia* had pubescent leaf sheaths. Most plants of both varieties have at least some pubescence on the collar or collar margins whether or not the sheath is pubescent. Sheath pubescence in *longifolia* is usually slight and mostly restricted to or heaviest at or near the margins, although plants occur with copious pubescence over the entire sheath. *Magna* sheaths are usually heavily pubescent, but may be

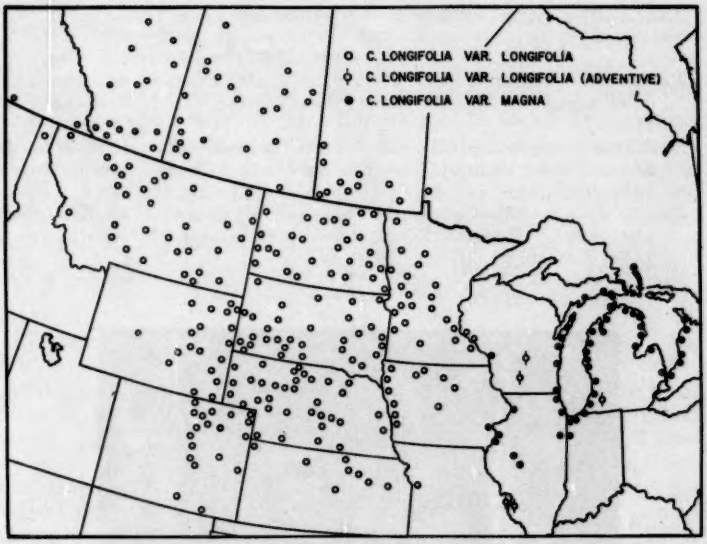

Fig. 2.—Distribution of *Calamovilfa longifolia.*

lightly so or rarely even glabrous (as in R. W. Pohl No. 1088, Kenosha Co., Wisconsin [MICH, MIN, WIS]).

Geographic distribution.—Var. *longifolia* is a characteristic grass of many drier prairies on the interior plains of the United States and southern Canada (Fig. 2). It is usually found in sand or sandy soil but occasionally in clay soil or loess. Its growth seems to be especially vigorous in disturbed soil. Its western limit coincides reasonably well with the western limit of the Great Plains province, although outlying stations occur in dry grasslands in the Cordilleran region. To the north the grass extends throughout the grassland and parkland of Canada's prairie provinces and enters slightly into the southern portion of the boreal forest where it occurs on sand dunes, sandy pinelands, and sandy prairies. It reaches a southern limit in southeast Colorado and an eastern limit in southwest Wisconsin. It has been found as an adventive in south central Wisconsin, the St. Louis area, and southwest Michigan.

Var. *magna* is a characteristic grass of dunes — especially those that are active and semi-established — and sandy shores fringing Lakes Michigan and Huron (Fig. 2). It is an excellent sand binder. Inland stations occur on sand or sandy soil in northwest Indiana, northeast, west and central Illinois, southeast Iowa, and southwest Wisconsin.

Noteworthy collections of *C. longifolia* are cited below.

C. longifolia var. *longifolia*

Northernmost collection (lat. 54° 20′ 30″). Waterhen River crossing 25 miles north of Meadow Lake, Saskatchewan, A. J. Breitung 8263 (DAO).

Southernmost collection (lat. 37° 10′ 10″). Sandy soil, side of Mesa de Maya, 3 miles south of Tobe, Las Animas Co., Colorado, C. M. Rogers 5031 (COLO).

New to British Columbia. Kettle Valley, British Columbia, H. K. DeBeck s.n. (UBC); Tobacco Plains, north of Flagstone, British Columbia, J. W. Eastham s.n. (DAO, US).

New to Ontario. Dry, gravelly soil, Ingolf [southwest] Ontario, W. N. Denike 1320 (DAO).

Fig. 3.—Panicles of var. *longifolia* (left) and var. *magna* (right) to show difference in density of inflorescence. The panicle of *longifolia* is an atypically open one.

C. longifolia var. *magna*

New to Iowa. Sand, Moose Lodge area, Muscatine Island, Louisa Co., Iowa, B. Shimek s.n. (ISC).

Density of the inflorescence.—An excellent criterion to distinguish the varieties is the density of the inflorescence. In *longifolia* the spikelets are relatively closely imbricated so that transverse lines laid across a branch usually cross 2 or 3 (sometimes 4) spikelets. In *magna,* on the other hand, usually only 1 or 2 spikelets are crossed because the spikelets are less closely imbricated. The relative density of the inflorescences of *longifolia* and *magna,* difficult to express verbally, can best be appreciated by observing the panicles themselves (see Fig. 3).

A description of *Calamovilfa longifolia* and a key to its varieties follow.

Calamovilfa longifolia (Hook.) Scribn. A coarse perennial grass, culms bunched or solitary, to 23.4 dm high, with elongate, scaly, pointed rhizomes and tough, wiry roots. *Leaves* rolled in the bud; sheaths to 15 cm in length, open, with mostly overlapping hyaline margins, glabrous to densely villous; blades to 64 cm long, 12 mm wide at the base, firm, flat to involute, tapering to a long thin tip; collar distinct, broad, continuous, yellowish, usually pubescent on the margins; ligule a dense fringe of hairs to 3 mm long. *Panicles* up to 77.5 cm in length, long-exserted to included at the base, contracted and narrow to open and broad, the branches tightly appressed to widely spreading, the lower sometimes reflexed. *Spikelets* awnless, to 8.5 mm long (usually 5-7 mm), basically straw color but often overlaid with varying amounts of violet-purple and/or brown; glumes acute, one-nerved, glabrous, subequal to unequal, the second the longer; lemma and palea subequal, glabrous, slightly shorter than, equal to, or longer than the second glume; lemma one-nerved, palea furrowed between its 2 nerves; callus densely bearded with silky hairs ½ to ⅞ the length of the floret; anthers 3 to 5 mm long.

KEY TO VARIETIES

Panicles mostly 1.3-5.5 times as long as wide, mostly 7.3 - 26.4 cm wide, up to 77.5 cm long. *Panicle branches* up to 33 cm long, typically widely spreading, diverging often more than 50° in the lower third of the inflorescence, sometimes reflexed. *Spikelets* commonly with a brownish cast, relatively loosely imbricated. *Leaf sheaths* usually pubescent, often densely so, rarely glabrous. Plant of the shores of Lakes Michigan and Huron, also outlying stations in southeast Iowa, in northeast, west, and central Illinois, in southwest Wisconsin, and in northwest Indiana.....var. *magna* Scribn. & Merr.

Panicles mostly 6.7 - 13.9 times as long as wide, mostly 1.7 - 4.3 cm wide, up to 55.5 cm long. *Panicle branches* up to 23 cm long, usually much shorter, typically appressed or strongly ascending, at least in the upper third of the inflorescence. *Spikelets* only rarely with brownish cast, relatively closely imbricated. *Leaf sheaths* mostly glabrous, infrequently lightly pubescent, rarely densely so. Plant ranging from extreme south-

west Ontario north and west to central Saskatchewan and Alberta, southeast British Columbia, south and west to southwest Wisconsin, northwest Missouri, southeast Colorado, east Wyoming, and northern Idaho, rarely adventive further east.....var. *longifolia*

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Correlation of a Population of Roof Rats in Venezuela with Seasonal Changes in Habitat

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The purpose of this study is to obtain a better understanding of the forces acting on the rodent population in Venezuela. The site of the study is Zorro Island in Lake Valencia (Tacarigua). This locality was chosen because it is inhabited by a colony of *Rattus rattus rattus,* the size is adequate, there is little possibility of migrations, and meteorological data are readily available. The study began April, 1956; it still continues but the data presented cover only the period from that date to January 1958.

Lake Valencia, in the North Central part of Venezuela is 33 km long, 18 km wide and has an average depth of 30 m. The level of the lake varies according to the season, but the average altitude of its surface is about 400 meters above sea level. There are 20 islands or protruding rocks.

Zorro Island is the fifth largest island and is located in the southeastern part of the lake (10° 09′N 67°39′W) (Fig. 1). Its maximum dimensions are 450 m by 225 m, and its area is 6.5 hectares. The maximum height above lake level is 43 m. The shortest distance to other land areas, the Iguana Peninsula, is 750 m. Actually the distances are rough averages for the duration of the study, as the shore line changes due to the seasonal fluctuations of about a meter in the level of the lake's surface. Also, the general trend is for this level to decrease, having lost about 20 m since 1727.

The island's origin has been traced to the Tertiary geological era. It was formed by projected masses of rocks and eruptive adjustments. The surface is composed of a steep central hill surrounded on the east, south, and west sides by a crescent-shaped, terraced, gradually-sloping area that has emerged due to the decrease of the level of the lake. Based on this formation the island can be divided into four general areas: (a) shore, narrow strip of rocks with occasional coarse sand beaches; (b) emerged zone, largest component of the study sites; the basic soil is an accumulation of loam, humus, pebbles and small rocks that increase in size towards the central hill. The average slopes are: east side 30 percent, south 16 percent, west 23 percent. There is an unusual narrow vein of sandy loam traversing the southern part; (c) central hill, steep, 74 percent slope and formed by clusters of large rocks based over a rock bed; (d) hilltop, rather flat and with a surface similar to that of the emerged zone suggesting that the entire island was covered by water at some ancient period.

Natural drainage of the island is excellent, and no surface water is found. The lake water is quite brackish with a pH value of 8.8

and a salinity of 1.1 ppm which is increasing at a yearly rate of 3.4 parts per million. Rainfall and temperature date for the years of trapping are given in Table I. The rain usually falls in intense periods of short duration separated by fair weather with clear sky. During the peak of the rainy season cloudy days with no direct sunlight may occur. The direction of the wind is quite varied over the lake, but predominantly from the east. Light breezes are normal during the early night and through the morning, changing to gales in the afternoon that produce short white-capped waves one meter or more in height. The intensity of the east wind appears to be uniform throughout the year. At the beginning of the rainy season this wind carries debris from the eastern mainland shore to the eastern shore of the island. The waste consists of tree branches, decomposed local crops,

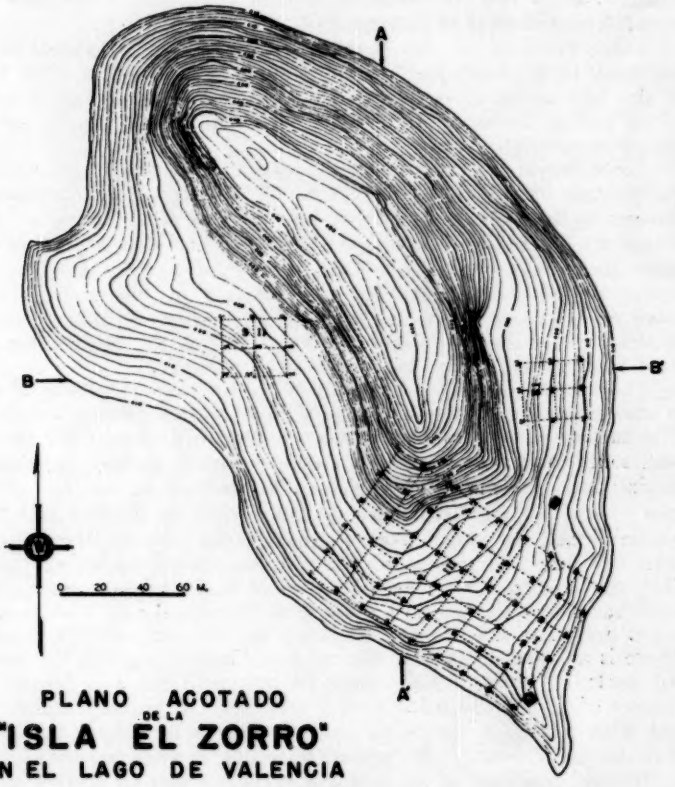

Fig. 1.—Contour map of Zorro Island showing location of grids.

and empty containers and could be the source of some of the animals and plants now living on the island.

VEGETATION

The vegetation of the island is a tropical, deciduous, seasonal forest similar to that of the near mainland. The submerged plants in the lake are represented by the genera *Chara, Nostoc, Potamogeton, Najas* and *Vallisneria* which form colonies close to the shore varying in density according to depth. The emergent vegetation is represented by one species of each genus, *Panicum, Acnida* and *Typha.* Their existence is governed by the fluctuations of the water level, the waves, and the soil. The floating vegetation consists of three genera, each represented by one species, *Pistia, Eichornia,* and *Hydromystria.* Their presence is determined by the winds and currents.

The *Paspalum-Poponax* Zone is a narrow strip of land along the island's perimeter, characterized by the dominant grass (*Paspalum*) in the lower level with occasional intrusion of emergent *Panicum.*

TABLE I.—Rainfall and temperature data for the months when trapping

Year	Month	Total Rainfall mm.	Mean Temp. °C	Mean Percent Humidity
1956	January	18.5	22.8	78
	February	13.5	23.8	74
	March	11.1	24.2	71
	April*	5.9	25.4	70
	May	81.1	25.3	76
	June	87.2	24.7	78
	July	71.1	23.9	81
	August	269.9	23.6	85
	September	104.2	23.8	83
	October	163.4	23.9	83
	November	61.2	23.7	81
	December	67.8	22.5	81
1957	January	6.5	21.8	76
	February	0.2	23.2	71
	March	0.0	24.4	67
	April**	16.3	25.5	69
	May	70.1	25.6	77
	June	88.6	24.6	81
	July	113.9	24.5	81
	August	198.3	24.3	81
	September	112.8	24.6	81
	October	77.6	24.1	81
	November	49.3	24.1	80
	December	1.2	24.4	73
1958	January	0.0	24.3	70

* rain for first time the last week of April
** rain for the first time the night of the 12th.

In the canopy the tree *Poponax* is abundant. Many vines, bromeliads, and other arboreal forms are present on these trees.

The *Capparis* Zone ranges up to the base of the central hill and is characterized by the great abundance of three species of *Capparis* forming an intermediate canopy. Also present are two species of cacti and an intricate group of vines (*Cissus, Serjania, Elaterium*) covers the trees and sometimes rocks and fallen trunks. Among the eleven species of smaller plants forming the underbrush by far the most numerous are *Petiveria* and young *Capparis.*

The *Bursera* Zone occurs around the base and slope of the central hill where the tall *Bursera* forms a dense canopy. Other large trees are found, including some unidentified legumes. The underbrush is similar to that in the *Capparis* zone, but is heavier and includes impenetrable barriers formed by great clusters of *Petiveria* and the thorny *Acanthaceae.*

The *Tabebuia* Zone at the crown of the hill consists of a dense colony of *Tabebuia,* up to 8.0 m in height, dominating over other vegetation formed mostly by *Cereus, Peireskia, Capparis, Bursera, Coccoloba,* and cacti. The underbrush is composed of a varied group of grasses; one of them, a very small type of bamboo, forms dense colonies.

The species occurring on the three sides of the hill show no striking differences in the small sample available along the transect. However, some minor differences occur between the vegetation of the hill and the surrounding zone (Table II). Nevertheless the area is considered sufficiently homogeneous in vegetation to permit its treatment as a unit for some aspects of the population description.

FAUNA

The fauna, like the flora, is a selection derived from the mainland species, and its origin is partly due to wind and water transportation as mentioned in the discussion of the meteorological data. It is beyond the scope of this study to give a complete list of the varied fauna on the island and only the most prominent will be mentioned. There are no Amphibia on the island. The amphibious reptiles are plentifully represented by a small alligator and some turtles, the latter introduced from the llanos. Also found are a great number of small

TABLE II.—Summary of some aspects of vegetation

	Part of Island				
	East	South	West	Hillside	Hilltop
Trees: Number per 10 m ^{2}	7.3	6.8	7.1	2.0	4.5
Average height (m)	5.0	5.6	5.8	8.0	7.0
*Canopy cover (percent)	85.0	75.0	95.0	60.0	70.0
Underbrush: Cover (percent)	36.0	41.0	63.0	95.0	80.0
Height (m)	0.3	0.8	0.9	1.5	0.5

* August at noon

lizards, mostly geckos and iguanas, and an unidentified species of nonpoisonous snake. The birds include water turkeys and kingfishers along the shore, and woodpeckers, doves, flycatchers, egrets, troupials, and oropendolas on the island. Among the many seasonal visitors are hawks, hummingbirds, vultures, blue-winged teal, and parrots.

At the beginning of the study opossums (*Didelphis marsupialis*) created a problem by springing, displacing, and occasionally damaging the traps. The problem was solved by building special traps and removing the captured opossums to other islands. A total of 7 individuals was caught during the first two months and after that no more were noticed. Other mammals present are a few colonies of bats and rodents, primarily of the genus *Rattus;* on rare occasions members of *Cricetinae* (species unidentified) and *Mus musculus* have been caught, released, and never observed again. The presence of *Cricetinae* is assumed to be due to sporadic immigration by natural means, while that of *Mus* is due to transportation by boat from the north shore of the lake.

SEASONAL CHANGES

The seasonal changes of the habitat on Zorro Island are marked. From the meteorological data (Table I) it can be observed that the average monthly rainfall is variable, with a high and stable humidity as is expected in a lake habitat. Although the average monthly temperatures present extremes of 3.8° C this range is insignificant when compared to the occasional 7.0° C daily variations. The length of daylight does not change much during the year on account of the proximity to the equator.

Detailed measurements of changes of vegetation and of food were considered too formidable a task for this study and therefore the general changes will be described from observations at each trapping period. The dry season starts in December and lasts till May (Table I). With a few exceptions this periodicity in occurrence is uniform throughout the years but the amount of rain in the rainy season is variable. In January the underbrush has disappeared, only its seeds remain. The trees, with such exceptions as *Ficus, Poponax, Hura* and *Capparis,* have shed all their leaves. Fruits are found in small quantity only on some *Bursera* and the ground is covered by a thick layer of dry leaves. The density of sunlight falling on the terrain has increased greatly. Also, as is common in this type of forest, during this month the trees begin to flower. Animal activity, with the exception of some reptiles and insects, starts to decrease. During February, the iguanas concentrate on the top of the central hill and deposit their eggs in shallow depressions which they excavate in the soft soil. In the following months the dryness increases, most trees are covered with flowers, and thus the island attracts numerous insects and hummingbirds searching for nectar. Below on the ground animal life is scarce and only the shore dwellers maintain their normal activities.

During March or April the first rains fall. Slowly, at first, the trees begin to produce new leaves and the flowers are replaced by fruits. This is also the time when young iguanas make their appearance and soon can be seen in great numbers. The increasing humidity of the ground accelerates the rotting process of the organic matter covering the soil and the land arthropods start to appear. By June, new underbrush is noticeable, and in July many birds can be seen eating fruits and insects and nesting on the island. The parrots are especially attracted by the great quantities of nest-building material offered by the abundant termite "hills." In August and September, the peak of the rainy season, the island is dark, humid, and covered by thick vegetation. The underbrush and vines form intricately harsh, some times poisonous and thorny, barriers that interfere with walking. To this can be added the presence of a considerable number of poisonous arachnids and other pests such as ticks and ants. Usually after September the amount of rain decreases steadily. The first notable change is the reduction in the number of trees with fruits. By November these have all but disappeared and the leaves begin to fall. At this time the underbrush is drying fast and the arthropods are becoming scarce. December marks the end of the rainy season; most trees are leafless and the only fruits, in small quantity and dry, are found on *Bursera*. The arthropods and underbrush are almost nonexistent and seeds from small plants can be seen on the ground. Again, animal activity decreases and the changes in conditions lead to a repetition of the yearly cycle already described. As far as known Zorro Island has not been inhabited by man and so it remains rather unaffected by human use.

METHODS

The data for the description of the area were obtained from observations and available sources. A complete topographical map of Zorro Island was made for the study using standard survey methods, based on 0.5 m contour curves. The soil description is based on surface observations. The meteorological data were supplied for Zorro Island by the meteorological service of the Venezuelan Air Force which maintains a number of stations around the lake. The description of flora, fauna, and their seasonal changes are based on personal observations. The quantitative estimates of leaves, flowers, fruits, and underbrush and seeds are based on the observation of 10 sample areas, each 15 x 15 m and distributed over the island.

The study of the *Rattus* population is based on the application of the methods, concepts, and assumptions described by Davis (1956). The descriptions that follow only apply to such cases where the method used or some specific detail differs from the text of Davis's manual. In general the method consisted of placing traps in a grid pattern. These traps were set and inspected each morning for 4 or 5 days each month. The captured rats are weighed, marked, inspected for sexual development, and released. The population estimate is

based on the proportion of recaptured individuals in each monthly sample.

The traps were placed on the southern part of the island in a normal grid of 6 x 9 lines 15 m apart. In the east and west they were in parallel lines at the same distance apart but only covering the available space. On the hill and north side a few traps were scattered to detect any presence of rats. A total of 137 traps was normally in use. The traps were rectangular in shape and approximately 35 x 11 x 11 cm in size. Peanut butter, corn, and other cereals

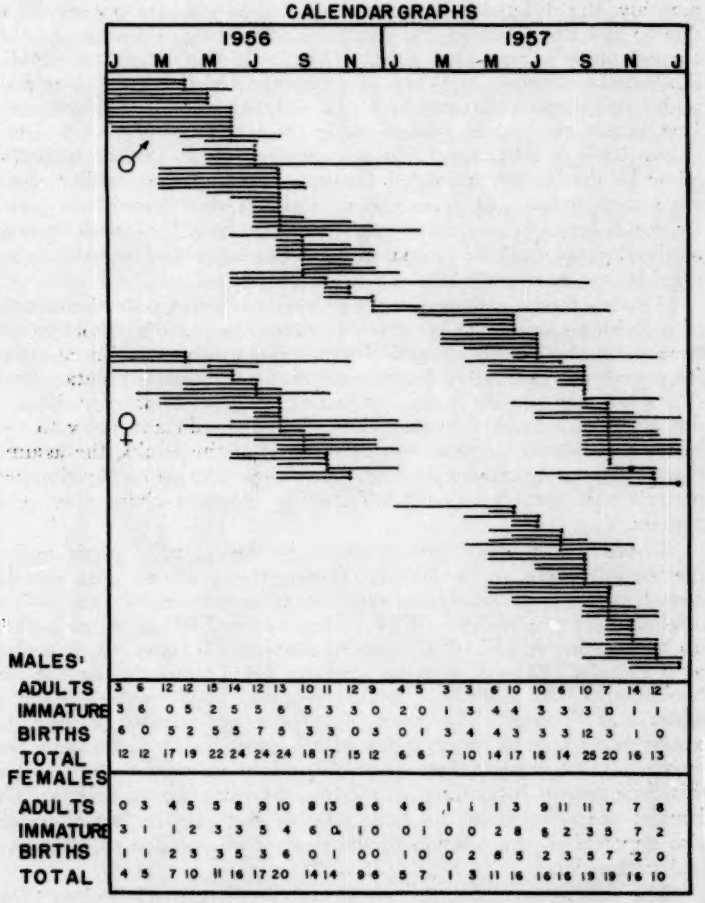

Fig. 2.—Calendar graph for rats (see text for explanation).

were used as bait during the first month, but the infestation of the traps by spiders, ants, and roaches made it necessary to search for another bait. A very suitable one was found in a local brand of rabbit food. This kept to a minimum the arthropods found inside the traps and was stable during the rainy season. The average number of traps accidentally sprung was about 3 percent. All traps were arranged to capture animals of 20 grams or more but on occasions two individuals of lighter weight have been caught by the same trap.

The populations were estimated in two ways. The first is based on the recapture method. However, although the results fluctuate monthly, the difference between those fluctuations are not significant due to the small size of the sample under study. Because of this a second method was also used. This "calendar graph" method is illustrated in Figure 2. When a rat is captured it is plotted as a dot under the corresponding month. Its weight and sexual development (see later) establishes approximately its month of birth. A line is drawn back to that month. Subsequent recaptures of that individual allow its line to be prolonged forward. To find the number of rats alive each month the lines passing through that month are added. By the distance of any point to the assumed month of birth the state of development of the animal can be estimated and the data separated by sex, age, and births.

This method presents some problems. It gives only the number of individuals known to be alive. It cannot be used for short periods because as the length of study increases, the chances of a recapture for a rat increases, thereby increasing the amount of data. Some difficulties are present when projecting the life of the rat back to the assumed month of birth. These difficulties do not apply to very young individuals but with the placements of the adults, the assumptions have to be made that all rats follow the same development pattern and that this is not affected by seasonal changes or pregnancies.

In order to estimate the population by the calendar graph method the growth needs to be known. Hence, the available data are discussed in the methods section rather than in the results section. The original data are weights of 31 males observed 94 times for periods up to 11 months and of 23 females observed 59 times up to periods of 6 months. Growth is quite uniform for all rats during the first two months. No difference is demonstrated between the growth of males and females. The rates of growth are affected by the dry season according to observations of 19 males followed through that season. In 12 males a loss up to 20 percent in weight was noted at this time, which is regained as soon as the rainy season arrives. The females are affected in the same manner but gain or loss of weight also depends on the relation of the time of observation to pregnancy and parturition.

The sample used for the given growth rates is selected to avoid the influence of the above mentioned factors. The approximated

growth rates for both sexes used in calculating the calendar graph were: 38 grams per month during first month, 27 grams per month for next 2 months, and 15 grams per month from 3 to 6 months.

For interpretation of population estimates and movements some information on susceptibility to capture is important. From Table III it is clear that the frequency of recapture is indistinguishable for the two sexes. Naturally no information is available for the proportion never captured.

RESULTS

Movement of Individuals.—At the beginning of the study only the traps at the southern side caught rodents but by the end of the year the focus of the population had drifted towards the north of the island. To demonstrate this movement quantitatively the percentages of individuals trapped were grouped in consecutive periods of 5 months each starting from April 1956 and ending in November 1957 (Table IV). The distance at which they were caught is given in relation to the hut at the southern tip of the island.

As can be seen the highest group percentage of individuals trapped moves progressively away from the south. These results are difficult to test statistically. However, several biological explanations would agree with the observations. It could be that the population had its origin at the southern shores and is spreading over the island. A few observations support this possibility. a) The *Cricetinae* occasionally trapped, and never seen again, were always found at the south of the island. If the assumption that they are new immigrants is correct, then whatever mode of transportation carried them there could also have carried the *Rattus* to the same place. b) Environmental conditions at the east and west sides are as good as, or better than, those at the south but no rats were found there during the early part of the

TABLE III.—Number of captures of males and of females

Times captured	Males			Females		
	Number	Percent	Cumulative	Number	Percent	Cumulative
1	46	51.6	51.6	30	46.9	46.9
2	16	18.0	69.6	19	29.7	76.6
3	13	14.7	84.3	9	14.1	90.7
4	4	4.5	88.8	2	3.1	93.8
5	4	4.5	93.3	0	0	93.8
6	4	4.5	97.8	0	0	93.8
7	1	1.1	98.9	2	3.1	96.9
8	0	0	98.9	2	3.1	100.0
9	0	0	98.9			
10	1	1.1	100.0			
Total	89			64		
Observations per rat	2.14			2.08		

study. No rat has been caught in the extreme northern part. The center hill appears to be a natural barrier for the rats. None has been trapped at the summit nor have any of those marked in the east or west been captured at the opposite side. Due to conditions emigration seems unlikely.

The movement of individuals was analyzed from the recaptures. The displacement distances increase numerically as the time interval between observations increases but the differences were not statistically significant. Most males were recaptured at the same trap, but some travelled up to 80 meters. Most females were recap-

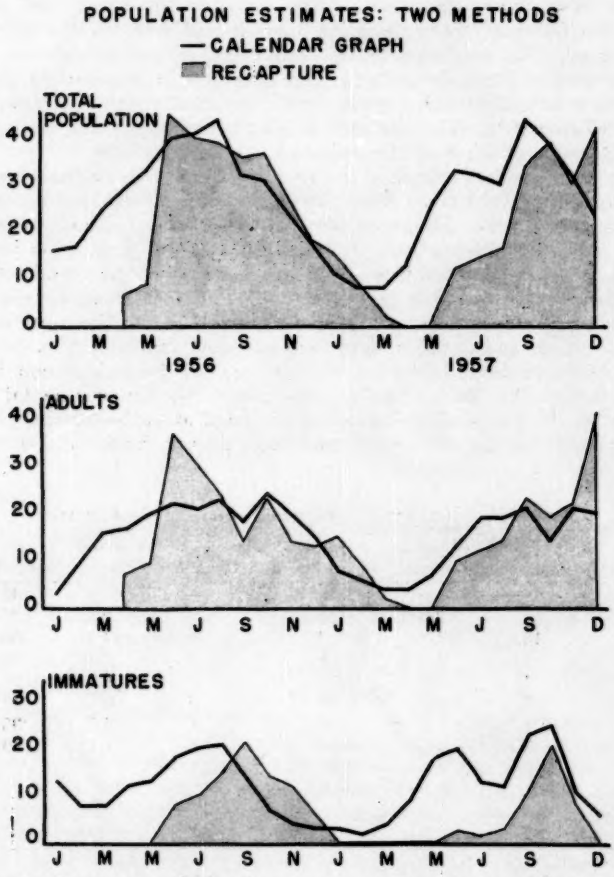

Fig. 3—Population estimates by recapture and by calendar graph methods.

TABLE IV.—Percentage of individuals trapped at distances at southern tip of island

Periods of Observation		Number of rats	Percentage by Distance in Meters 0-15	50-100	100-150	150+
I	April-August	59	29	20	24	27
II	September-January	75	27	31	21	21
III	February-June	14	15	21	43	21
IV	July-November	77	13	7	27	53

tured from 15 to 20 meters away from the original trap, but not much farther. This suggested sexual difference in movement might be induced by the care that the females must give to their young in the nests. The meager data collected for the immatures only hints that their movement is limited. So few observations were recorded during the dry season that no seasonal comparison was possible.

Population Changes.—The two methods used for the population

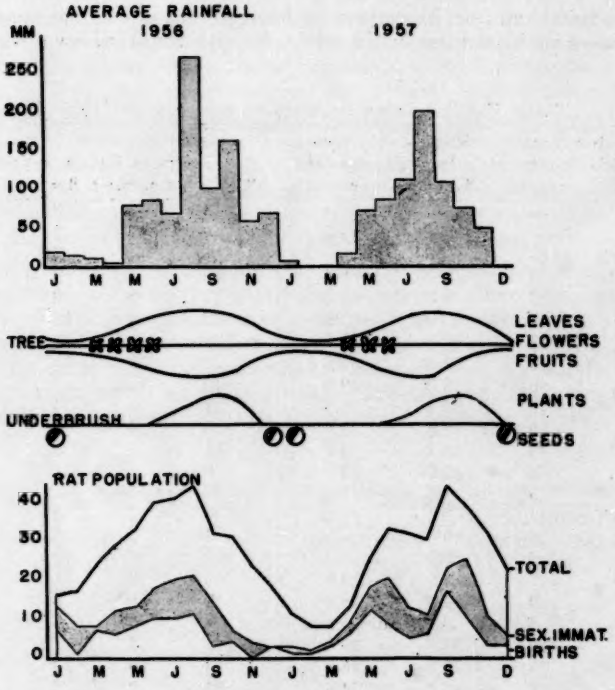

Fig. 4.—Comparison of rainfall and vegetation with rat population.

estimate give similar results (Table V). Figure 3 compares the seasonal variations observed in both the sexually immature and total populations as shown by the two methods. In general the recapture method reports the fluctuations at a later time than does the calendar graph method. This could have resulted from the following: (a) The individual rate of growth is greater than assumed, or (b) since the recapture method deals only with trappable individuals which are above certain weight, while the other method includes them from the moment of birth, a gap is created between the results. This gap is the time required from birth for a rat to become trappable. From the observed individual growth and the fact that not all rats are caught immediately upon reaching the required weight to spring a trap, it is assumed that the lag of the recapture method occurs mostly on account of the second reason given.

The changes in the population curve (Fig. 4) appear to be dependent on the seasonal quantity of animal and vegetable food available to the rats. The curves representing the population for the year 1956 and 1957 are not markedly different. However, in 1956 there is only one peak in the curve while two are present in 1957 for adults and for immatures. Although this difference cannot be demonstrated statistically, it might be the result of two waves of

TABLE V.—Population estimates by two methods (1956-57)

Month (1956-1957)	Total rats caught	Recapture Estimate	Two standard errors	Calendar Graph Estimate			
				Adults	Immatures	Born	Total
Jan.	—	—	—	3	6	7	16
Feb.	—	—	—	9	7	1	17
March	—	—	—	16	1	7	24
April	6	6.7	5.3	17	7	5	29
May	5	9.0	15.0	20	5	8	33
June	13	45.0	85.0	22	8	10	40
July	13	40.0	75.0	21	10	10	41
Aug.	27	39.0	24.0	23	10	11	44
Sept.	20	36.0	29.0	18	11	3	32
Oct.	18	36.7	36.3	24	3	4	31
Nov.	15	25.6	22.4	20	4	0	24
Dec.	15	18.3	9.7	15	0	3	18
Jan.	8	15.0	25.0	8	2	1	11
Feb.	5	9.0	15.0	6	1	1	8
March	2	2.0	3.0	4	1	3	8
April	0	0.0	—	4	3	6	13
May	0	0.0	—	7	6	12	25
June	6	12.0	19.6	13	12	8	33
July	9	14.0	19.8	19	8	5	32
Aug	7	No recaptures		19	5	6	30
Sept.	19	33.8	29.0	21	6	17	44
Oct.	25	39.0	26.0	14	15	10	39
Nov.	18	30.0	24.6	21	8	3	32
Dec.	18	42.0	48.4	20	3	0	23

reproduction, the first from the survivors of the dry season and the second from their progeny.

It is apparent that the initial population was greater in 1956 than in 1957, and hence the peak 1956 population should have been greater than that of 1957. However, the peak population was essentially the same for the two years. Examination of the data suggests that a consideration of the area may provide the explanation. If it is true that the colony is recent and still spreading from its origin at the southern part of the island, then the area occupied by the rats was much greater in 1957 than in 1956. In Table VI it can be seen that in 1956 the grid at the south reached a population nearly twice as large as that of 1957. The population pressure thus created presumably induced more individuals to move north, but then the dry season arrived and stopped the population increment that should have resulted from the presence of rats in other suitable parts of the island.

In 1957 the rats were more evenly distributed over the island, but there are so few individuals left at the beginning of the rainy season that peak local density at the south grid was small.

Distribution.—Observations based on the total number of individuals captured by each trap show that the distribution is correlated with the characteristics of soil and vegetation. The highest population occurs in areas with heavy upper canopy and in the presence of *Peireskia, Cereus, Sapindus,* and other fruit trees where the terrain is relatively clear and rocky. The absence of captures in the center of the population in the south of the island is notable. In this place a very sandy zone is used occasionally for egg-laying by the iguanas. Except in this sandy zone the island's surface offers more than adequate shelter for a population greater than the observed.

Probabilities of Reappearance and Survival.—The recapture method does not give the probability of survival directly because it is not possible to conclude that a rat that is not captured is dead. Although there is a method to calculate probability of survival from recapture data, the small numbers in this study would result in such a large variance that no differences could be demonstrated. However, some biological information can be extracted from the reappearance

TABLE VI.—The maximum population based on two estimate methods

Recapture method:	1956 June-August	1957 September-December
Total for island	41.4	38.2
South grid only	29.5	15.8
Percent in south grid	71.3	41.3
Calendar graph (adults only)		
Total adults for island	19.5	20.7
South grid only	12.3	7.7
Percent in south grid	63.1	37.2

of rats in traps. The 29 males and the 21 females (Table VII) that were recaptured at least once were tallied irrespective of season or age according to the number of months between the first and the last capture. For example 42 percent of the males were not captured after the first recapture and 65 percent after the second. In the other part of Table VII the probability of survival from the calculated birth is recorded. Each rat when captured was aged by its weight and then assigned to a month of birth. In this manner the age at last capture was obtained for 82 males and 61 females. The survivals are a minimum because the rats lived for an unknown time after last capture. As expected the probability of reappearance is less than the minimum probability of surviving (Table VII). Because both probabilities are affected by seasonal changes it is superfluous to express them as yearly rates.

The chances of surviving for rats born in the dry season have been compared with survival of those born in the wet season (Table VIII). Rats born in the dry season should survive better (if they reach trappable age), because in about 4 months they would live in the presumably favorable conditions of the wet season. In contrast rats born in the wet season would encounter unfavorable conditions in a few months. Since the difference between probabilities at 3-5 months is statistically significant it can be concluded that the dry season influences the life expectancy of the rats.

Breeding Conditions.—The data available from the trapping (Table IX) were tabulated into four arbitrary seasons that include the following months: (a) Dry: April of 1956, January, February, March and April of 1957. (b) Before rainy: May and June of

TABLE VII.—Reappearance and survival of rats

Months since first capture	Probability of reappearance in traps		Months known to be alive	Probability of survival from calculated birth	
	29 males	21 females		82 males	61 females
1	1.00	1.00			
2	0.58	0.68	1	1.00	1.00
3	0.35	0.43	2	0.85	0.77
4	0.18	0.19	3	0.68	0.59
5	0.12	0.14	4	0.56	0.41
6	0.09	0.09	5	0.37	0.28
7	0.09	0.05	6	0.05	0.13
8	0.09	—	7	0.04	0.09
9	0.06	—	8	0.04	0.07
10	0.06	—	9	0.04	0.05
11	0.03	—	10	0.01	0.03
			11	0.01	
			12	0.01	
			13	0.01	
			14	0.01	
			15	0.01	

TABLE VIII.—Seasonal differences in minimum probability alive

Months known to be alive	Season of birth: Dry January-June 69 rats	Season of birth: Wet July-December 81 rats
0	1.00	1.00
1	1.00	0.93
2	0.90	0.72
3	0.77	0.47
4	0.68	0.33
5	0.39	0.19
6	0.16	0.06
7	0.10	
8	0.06	
9	0.04	
10	0.04	
11	0.01	

1956, May, June and July of 1957. (c) Rainy: July, August and September of 1956, August, September and October of 1957. (d) After rainy: October, November and December of 1956, November and December of 1957, January of 1958. The months were grouped according to the similarity in their environmental and population characteristics.

The males caught during the dry season were all sexually mature (Table IX). The estimate of the weight at which 50 percent are mature has a low value of less than 50 grams (Fig. 5). In the next season, although some immature individuals are present, the maturity midpoint increases. Presumably a better food supply allows the rats to gain weight and thus weigh more when attaining sexual

TABLE IX.—Breeding conditions of rats by seasons

	Dry	Before Rainy	Rainy	After Rainy	All Seasons
Rats Observed					
Males	13	22	63	55	153
Females	5	12	48	37	102
Total	18	34	111	92	255
Percent Sexually Mature					
Males	100.0	91.0	41.3	74.5	65.3
Females	100.0	75.0	81.3	75.6	79.5
Percent Lactating					
Females	80.0	41.7	69.0	19.0	38.3
Midpoint for Sexual Maturity					
Males	50 g	70 g	103 g	67 g	77 g
Females	90 g	68 g	57 g	60 g	60 g

maturity. In the rainy season a large number of immatures occur in the population and the maturity midpoint increases denoting a rapid increase in individual size. The data for rats captured after the rainy season are similar to the dry season thus giving continuity to the cycle. The females show the same correlations mentioned for the males with the exception of the sexual maturity midpoints.

The data from individual growth show that about two months after birth the rats attain sexual maturity (Table IX) in both sexes.

From Table IX and Figure 5, it can be deduced that the average weight is influenced by season (presumably through food supply) and by the number of young individuals in the population.

SUMMARY

The general purpose of a study of Roof Rats (*Rattus rattus*) was to consider the correlation of seasonal fluctuations of the habitat on the rat population in respect to the population size, distribution, growth, movement, and probabilities of survival in an insular population in Venezuela. Zorro Island has an area of 6.5 hectares and is

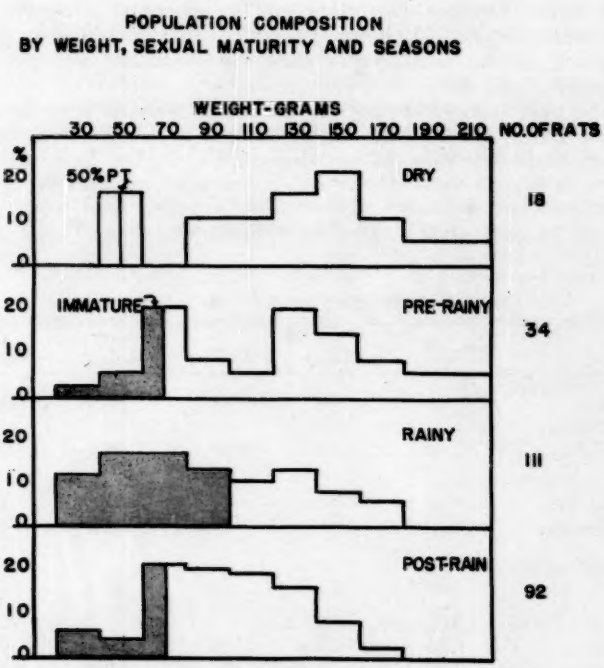

Fig. 5.—Composition of population in various seasons.

separated from the nearest shore by a distance of 750 meters. Its abrupt terrain is covered by a dense tropical deciduous seasonal forest. Besides the rats, other mammals found are bats and occasionally opossums. A great variety of birds and reptiles completes the fauna. The conclusions are based on the observations obtained from the systematic capture, marking, and release of individuals during a period of two years. A total of 153 different rats, 89 males and 64 females, were observed 327 times. No difference was noted between the trapability of males and females. Although the individual growth rate of the rats varies according to season, the average for both sexes ranges from 38 grams during the first month to 15 grams per month during the period between 3 and 6 months.

Great seasonal changes affect the environment; maximum rainfall occurs in August reaching a monthly precipitation of about 200 mm, while during the first three months of the year there is slight or no rainfall. The temperature and humidity do not suffer such extreme fluctuations. These changes presumably produce unevenness in the supply and distribution of food, thus creating marked seasonal variations in the characteristics of the ecosystem's biotic components.

During the rainy season the number of rats reached a maximum of about 40 on the island, later declining to about 10 at the end of the dry season. These individuals are not evenly distributed over the island. Furthermore the distribution also varies according to the supply of food and shelter. Immigration occurs on rare occasions, but emigration is unlikely due to local conditions. Individual movement appears greater for the males than for the females. During the dry season only sexually mature rats were observed but during the rainy season many immatures are present. Breeding occurs throughout the year. Sexual maturity is reached at a weight of about 70 grams and at an age varying from 1.5 to 2.5 months.

The life expectancy appears to be influenced by the relation of the month of birth to the seasons. Rats born in the dry season survived through the wet period but few born in the wet season survived through the dry. Although some rats were observed during periods as long as 15 months the average life expectancy is about 5 months.

REFERENCE

DAVIS, DAVID E. 1956. *Manual for the Analysis of Rodent Populations.* Ann Arbor: Edwards Bros. 82 pp.

A Study of the Population of Insects Emerging as Adults from South Walker Pond at London, Ontario[1]

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During the summer of 1956 a study was undertaken of the population of insects emerging as adults from South Walker Pond near London, Ontario. This pond is one of a group of three "kettle lakes" situated just south of London in Westminster Township and lying just to the northeast of the corner of Wellington Road and the road separating Concession 1 from Concession 2 of the Township. The three ponds are together designated as "The Ponds" by Saunders and Dale (1933) and as "Walker Ponds" on the maps of the National Topographic Series. The most easterly pond is "Spettigues' Pond," the most westerly one is "Saunders' Pond" and the most southerly one is "South Pond" or South Walker Pond. South Walker Pond (Fig. 1) is about 800 feet wide in the east-west direction and 800 feet in the north-south direction with three large bays extending easterly, westerly and southerly from the center of the lake. In the summer of 1956 there was no submerged or floating vegetation on the pond and the bottom was covered with the soft, brown remains of disintegrating leaves. The whole shore of the pond is surrounded by a deciduous wood which is most extensive towards the southeast.

Acknowledgment.—The writer is grateful to Mr. R. B. Catalan who aided daily during the summer of 1956 in collecting insects and in recording data. The Western Ontario Fish and Game Protective Association, on whose property South Walker is located, kindly granted permission for the study of the pond to be undertaken and supplied a boat, wharfing facilities and storage space during 1956.

Methods

Insects were trapped in a floating tent-trap set out on the water at each of five collection sites (Fig. 1). The trap was of the type described by Judd (1957), built to enclose four square feet of water surface. The trap was kept in one position during the course of the investigation and was held there by a rope anchored at one end to bricks on the bottom of the pond and stapled at the other end to the side of the trap.

The pond was completely covered with ice during 1956 until April 5. After that date thawing occurred and by April 10 the whole pond was free of ice. On April 10, the five traps were anchored in position, No. 1 one hundred and twenty feet from the north shore on

[1] Contribution from the Department of Zoology, University of Western Ontario; a project supported by funds from the Ontario Research Foundation.

[2] Associate Professor of Zoology.

water 23 feet deep, No. 2 fifteen feet from the west shore on water 5 feet deep, No. 3 twenty-four feet from the east shore on water 15 feet deep, No. 4 twenty-four feet from the south shore on water 5 feet deep and No. 5 one hundred and twenty feet from the southeast shore on water 24 feet deep (Fig. 1).

Each day the insects caught in each trap were collected. One side of the trap was raised above the surface of the water and an aspirator was passed into the trap and small insects were sucked into it. Larger insects, such as damsel flies, were picked from the lower surface of the screen of the trap with the fingers. The insects so collected were put into a killing jar and taken to the laboratory for sorting, counting, pinning (or preserving in fluid) and labelling. The depth of the water at each trap was measured each day and the maximum and minimum temperatures of the water for the previous 24-hour period at the bottom were taken at each trap with a Taylor Six's maximum-minimum thermometer. The thermometer was attached to the trap by a rope and was drawn up to the surface to be read. The traps were removed from the water and the last readings of temperature and depth were recorded on November 3.

The various groups of insects were identified by the following taxonomists who, unless otherwise noted, are or were staff members of the Entomology Research Division, United States Department of

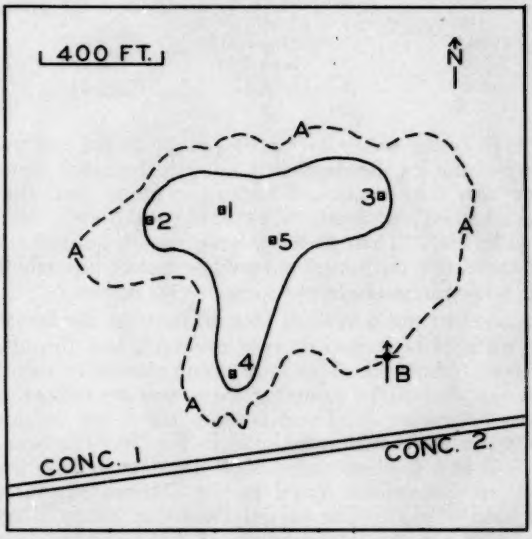

Fig. 1.—Map of South Walker Pond showing location of the five tent-traps (1-5). A—A: outer limit of deciduous wood. B: location of co-ordinate point 42° 57′ 45″ N, 80° 13′ W.

Agriculture: C. P. Alexander, University of Massachusetts (Tipulidae), R. S. Beal (Bruchidae), R. H. Foote (Dolichopodidae, Empididiae, Itonididae), F. P. Ide, University of Toronto (Ephemeroptera), C. F. W. Muesebeck (Braconidae), J. G. Rozen (Anthicidae, Dascyllidae), C. W. Sabrosky (Milichiidae, Sphaeroceridae), R. I. Sailer (Hemiptera), A. Stone (Culicidae, Psychodidae, Scatopsidae), G. B. Vogt (Chrysomelidae), E. M. Walker, Royal Ontario Museum, Toronto, Ontario (Odonata), R. E. Warner (Curculionidae), G. B. Wiggins, Royal Ontario Museum (Trichoptera), W. W. Wirth (Drosophilidae, Ephydridae, Heleidae, Tendipedidae).

All specimens are retained in the collections of the Department of Zoology, University of Western Ontario except as noted (USNM—United States National Museum; ROM—Royal Ontario Museum) in the following account.

PHYSICAL DATA

The measurements of temperature and water depth at the five traps were as follows:

Trap	Day-degrees by Nov. 3	Average Temperature Maximum — °C	Maximum Depth May 15 (inches)	Minimum Depth August 4 (inches)
1	1087	6.1 (October 22)	305	257
2	3390	24.5 (August 20)	92	44
3	3431	25.0 (August 15)	209	161
4	3591	25.6 (June 23)	99	51
5	1133	6.7 (July 17)	317	273

The depth of the water fluctuated equally at the five traps. After the melting of the ice the depth fell a few inches until April 27 (Fig. 2a). After this date continued melting of snow and the onset of spring rains caused the depth to increase steadily to a maximum on May 15 (Fig. 2a). Then the depth decreased until the middle of June and thereafter fluctuated only a few inches through the rest of the season, with minimum depths occurring on August 4.

The maximum and minimum temperatures on the bottom at each trap over each 24-hour period were averaged and the averages for each day were tabulated. The total accumulation of day-degrees at each cage was derived by summing these average temperatures from April 12 to November 3. These accumulations are included in the table above and are shown graphically in Fig. 2c. The accumulations at Traps 2, 3 and 4 all exceeded 3000 day-degrees and are comparable to the accumulations found in the Dundas Marsh in shallow water by Judd (1953). The accumulations at Traps 1 and 5 were much less, owing to the establishment of a thermocline in the pond. Temperature readings taken at various depths from the surface downward near Trap 5 on October 6 showed the epilimnion extending down to 12 feet, the thermocline extending from 12 feet to 21 feet

and the hypolimnion below 21 feet (Fig. 3). Thus Traps 1 and 5 were set over water including the hypolimnion and Traps 2, 3 and 4 over water above the hypolimnion. The average daily temperatures at Traps 2, 3, and 4 increased gradually during the season to values above 24°C (Fig. 2b) and remained fairly constant through June, July and August and decreased gradually in the fall. The temperature at Traps 1 and 5 increased very slightly during May and remained below 7°C during the season (Fig. 2b).

ACCOUNT OF TOTAL CATCH

The numbers of the various insects collected in the traps are presented in Table I and the numbers of insects in the seven orders collected are presented in Table II. During the whole period that the traps were in operation, April 10 to November 3, 4,108 insects were trapped. Most of the insects are species whose larvae or nymphs live

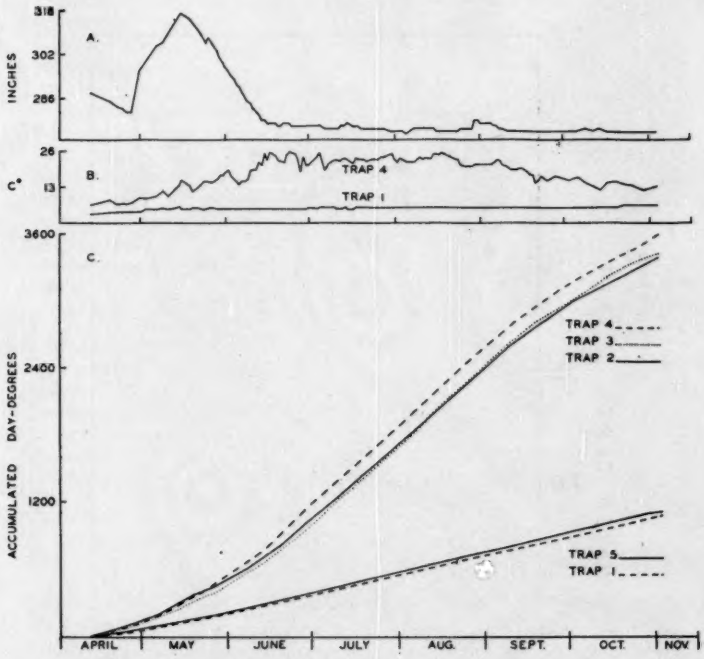

Fig. 2.—A. Water depth at Trap 5.—B. Average water temperature at bottom of pond at locations of Traps 1 and 4. C. Accumulated day-degrees at the bottom at locations of the five traps.

submerged and whose adults emerge from the water, but a few are insects that dwell on aquatic vegetation. The great majority (97%) were Diptera and among these the Tendipedidae predominated (82.5%). Next in point of numbers (15.8%) were the Culicidae. The other families of Diptera and the other orders were present in much smaller numbers.

The most productive sites were at Traps 3 and 4, yielding more than half the total catch. The area of water surface covered by each trap was 4 sq. ft., so the total area from which insects were collected was five times this area, 20 sq. ft. Over the whole season, 4,108 insects were trapped, a yield of 205.4 insects per sq. ft. The first insects emerged on May 4 and the last on October 22 (Fig. 4). The maximum peak of emergence occurred on June 7 (74 insects) owing largely to a big emergence of *Cricotopus bicinctus* (Fig. 5). Three other peaks of emergence occurred on July 11 (64 insects), August 14 (62 insects) and September 7 (65 insects). The catch decreased considerably in October. The distribution of species with respect to the hypo-

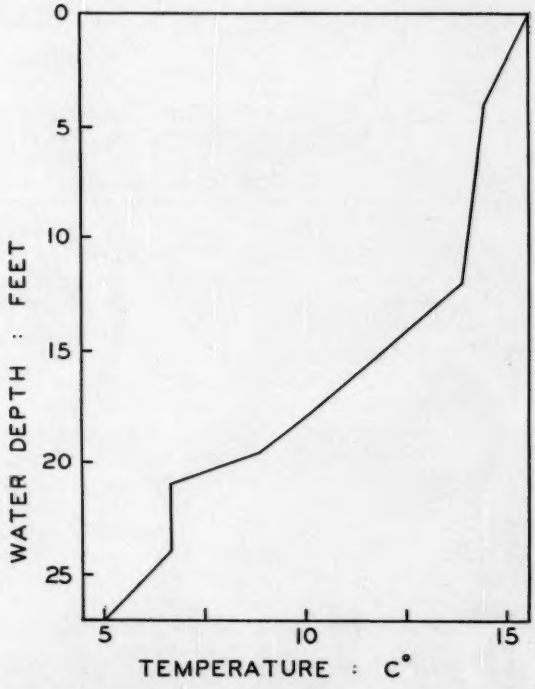

Fig. 3.—Temperature profile of water of pond on October 6 near Trap 5.

TABLE I: Numbers of insects collected in traps

	Trap 1		Trap 2		Trap 3		Trap 4		Trap 5		
	No.	%	No.	%	No.	%	No.	%	No.	%	Total
EPHEMEROPTERA											
BAETIDAE											
Callibaetis ferrugineus	0	0	0	0	0	0	2	100	0	0	2
Baetis pygmaeus	7	19	1	3	13	32	11	29	6	17	38
Caenis sp.	0	0	0	0	1	100	0	0	0	0	1
ODONATA											
COENAGRIIDAE											
Enallagma vesperum	0	0	0	0	0	0	1	100	0	0	1
TRICHOPTERA											
PSYCHOMYIIDAE											
Polycentropus cinereus	2	5	6	13	22	48	12	25	4	9	46
Polycentropus (?interruptus)	0	0	0	0	3	100	0	0	0	0	3
Nyctiophylax vestitus	0	0	0	0	1	33	2	67	0	0	3
HYDROPSYCHIDAE											
Hydropsyche (?simulans)	0	0	1	33	0	0	0	0	2	67	3
Cheumatopsyche sp.	1	7	0	0	4	3	8	62	0	0	13
LEPTOCERIDAE											
Oecetis inconspicua	0	0	0	0	2	50	2	50	0	0	4
Oecetis cinerascens	0	0	0	0	0	0	1	100	0	0	1
HEMIPTERA											
SALDIDAE											
Saldula confluenta	0	0	0	0	0	0	1	100	0	0	1
MESOVELIIDAE											
Mesovelia mulsanti	0	0	0	0	1	33	0	0	2	67	3
COLEOPTERA											
DASCYLLIDAE											
Ectopria sp.	0	0	0	0	0	0	2	100	0	0	2
CHRYSOMELIDAE											
Longitarsus sp.	0	0	1	100	0	0	0	0	0	0	1
ANTHICIDAE											
Notoxus sp.	0	0	0	0	0	0	0	0	1	100	1
BRUCHIDAE											
Bruchus brachialis	1	100	0	0	0	0	0	0	0	0	1

TABLE I.—(*continued*)

	Trap 1		Trap 2		Trap 3		Trap 4		Trap 5		Total
	No.	%	No.	%	No.	%	No.	%	No.	%	
CURCULIONIDAE											
Calendra sp.	0	0	0	0	0	0	1	100	0	0	1
DIPTERA											
TIPULIDAE											
Limonia canadensis	0	0	1	100	0	0	0	0	0	0	1
Helius flavipes	0	0	0	0	1	100	0	0	0	0	1
PSYCHODIDAE											
Psychoda lativentris	0	0	2	100	0	0	0	0	0	0	2
TENDIPEDIDAE											
Pentaneura monilis	3	1.5	40	17	62	27	125	54	1	0.5	231
Pentaneura sp.	9	12	14	18	10	12	21	26	26	32	80
Pelopia stellata	0	0	3	21	6	43	4	29	1	7	14
Clinotanypus thoracicus	0	0	0	0	0	0	5	100	0	0	5
Anatopynia dyari	1	100	0	0	0	0	0	0	0	0	1
Procladius culiciformis	32	8	73	20	70	20	142	39	46	13	363
Procladius bellus	10	8	23	15	25	15	72	50	14	12	144
Hydrobaenus sp.	2	10	1	4	16	76	2	10	0	0	21
Cricotopus trifasciatus	1	33	0	0	0	0	1	34	1	33	3
Cricotopus bicinctus	28	13	0	0	62	28	7	3	124	56	221
Microtendipes pedellus	0	0	10	8	85	66	22	17	11	9	128
Polypedilum sp.	4	5	11	20	30	50	12	20	4	5	61
Tanytarsus nigricans	82	18	47	11	191	42	79	17	54	12	453
Tendipes dux	0	0	0	0	0	0	5	100	0	0	5
Tanytarsus punctipes	0	0	4	6	35	63	11	20	6	11	56
Tendipes nervosus	56	66	25	30	4	4	0	0	0	0	85
Tendipes riparius	0	0	0	0	1	17	5	83	0	0	6
Glyptotendipes lobiferus	9	6	14	11	60	47	44	34	3	2	130
Glyptotendipes brachialis	0	0	0	0	7	100	0	0	0	0	7

TABLE I.—(*continued*)

	Trap 1		Trap 2		Trap 3		Trap 4		Trap 5		
	No.	%	No.	%	No.	%	No.	%	No.	%	Total
Stenochironomus hilaris	0	0	0	0	73	75	24	25	0	0	97
Calopsectra sp.	15	1	158	13	489	42	446	38	67	6	1,175
HELEIDAE											
Atrichopogon sp.	2	9	2	9	11	44	4	19	4	19	23
Bezzia glabra	2	13	5	34	2	13	6	40	0	0	15
Bezzia sp.	0	0	2	40	2	40	1	20	0	0	5
Culicoides piliferus	0	0	3	60	1	20	0	0	1	20	5
Palpomyia slossonae	0	0	0	0	1	100	0	0	0	0	1
CULICIDAE											
Chaoborus punctipennis	73	13	68	12	130	24	130	24	150	27	551
Chaoborus flavicans	32	43	7	10	9	12	5	8	20	27	73
ITONIDIDAE											
Itonidini	0	0	3	100	0	0	0	0	0	0	3
SCATOPSIDAE											
Scatopse fuscipes	0	0	1	100	0	0	0	0	0	0	1
DOLICHOPODIDAE											
Dolichopus sp.	0	0	0	0	2	100	0	0	0	0	2
Tachytrecha sp.	0	0	0	0	0	0	1	100	0	0	1
EMPIDIDAE											
Tachypeza sp.	0	0	0	0	0	0	1	100	0	0	1
EPHYDRIDAE											
Hydrellia sp.	0	0	3	60	1	20	0	0	1	20	5
Scatella picea	0	0	0	0	2	66	0	0	1	34	3
SPHAEROCERIDAE											
Leptocera wheeleri	0	0	0	0	0	0	0	0	1	100	1
DROSOPHILIDAE											
Drosophila melanogaster	0	0	0	0	0	0	1	100	0	0	1
MILICHIIDAE											
Desmometopa sordida	0	0	0	0	0	0	1	100	0	0	1
HYMENOPTERA											
BRACONIDAE											
Apanteles plethypenae	0	0	0	0	0	0	0	0	1	100	1
TOTALS	372	9	529	13	1,435	35	1,220	30	552	13	4,108

TABLE II: Number of insects of the seven orders collected in the traps

Group	Trap 1 No.	Trap 1 %	Trap 2 No.	Trap 2 %	Trap 3 No.	Trap 3 %	Trap 4 No.	Trap 4 %	Trap 5 No.	Trap 5 %	No.	% of Diptera	No.	% of Total
EPHEMEROPTERA	7	17	1	2	14	34	13	32	6	15			41	0.99
ODONATA	0	0	0	0	0	0	1	100	0	0			1	0.02
TRICHOPTERA	3	4	7	10	32	44	25	34	6	8			73	1.77
HEMIPTERA	0	0	0	0	1	25	1	25	2	50			4	0.08
COLEOPTERA	1	17	1	16	0	0	3	50	1	17			6	0.12
DIPTERA														
Tipulidae	0	0	1	50	1	50	0	0	0	0	2	0.05		
Psychodidae	0	0	2	100	0	0	0	0	0	0	2	0.05		
Tendipedidae	252	8	423	13	1,226	37	1,027	31	358	11	3,286	82.5		
Heleidae	4	8	12	25	17	35	11	22	5	10	49	1.2		
Culicidae	105	17	75	12	139	22	135	22	170	27	624	15.8		
Itonididae	0	0	3	100	0	0	0	0	0	0	3	0.07		
Scatopsidae	0	0	1	100	0	0	0	0	0	0	1	0.03		
Dolichopodidae	0	0	0	0	2	67	1	33	0	0	3	0.07		
Empididae	0	0	0	0	0	0	1	100	0	0	1	0.03		
Ephydridae	0	0	3	37	3	37	0	0	2	26	8	0.2		
Sphaeroceridae	0	0	0	0	0	0	0	0	1	100	1	0.03		
Drosophilidae	0	0	0	0	0	0	1	100	0	0	1	0.03		
Milichiidae	0	0	0	0	0	0	1	100	0	0	1	0.03		
Total Diptera	361	9	520	13	1,388	35	1,177	30	536	13	3,982	100.0	3,982	97.00
HYMENOPTERA	0	0	0	0	0	0	0	0	1	100			1	0.02
TOTALS	372	9	529	13	1,435	35	1,220	30	552	13			4,108	100.00

limnion (excluding Coleoptera, Hemiptera, Hymenoptera, Sphaeroceridae, Drosophilidae and Milichiidae) is as follows:

1. In hypolimnion:
   Anatopynia dyari

2. Mostly in hypolimnion:
   Cricotopus bicinctus

3. Mostly above hypolimnion:
   Pentaneura monilis
   Pelopia stellata
   Microtendipes pedellus
   Tanytarsus punctipes
   Glyptotendipes lobiferus

4. Above hypolimnion:
   Callibaetis ferrugineus
   Caenis sp.
   Enallagma vesperum
   Nyctiophylax vestitus
   Oecetis inconspicua
   Limonia canadensis
   Helius flavipes
   Psychoda lativentris
   Clinotanypus thoracicus
   Tendipes dux
   Tendipes riparius
   Glyptotendipes brachialis
   Stenochironomus hilaris
   Palpomyia slossonae
   Scatopse fuscipes
   Dolichopus sp.
   Tachytrecha sp.
   Tachypeza sp.

All other species were well distributed above and within the hypolimnion.

ACCOUNT OF SPECIES COLLECTED

EPHEMEROPTERA

BAETIDAE

Callibaetis ferrugineus Walsh.—2 mayflies (Trap 4: July 21, August 1).

Baetis pygmaeus Hagen—38♀♀ (Fig. 4) June 15-September 5, maximum July 7 (9 insects). *B. pygmaeus* is recorded from Ontario by Needham *et al.* (1935).

Caenis sp.—1 mayfly (Trap 3: August 19).

ODONATA

COENAGRIIDAE

Enallagma vesperum Calvert.—1 damsel fly (Trap 4: June 24). *E. vesperum* has been recorded from Ontario by Whitehouse (1948). The date of emergence of the specimen from South Walker Pond falls within the period, June 18-August 30, which Whitehouse records as the flight period of this species.

TRICHOPTERA

PSYCHOMYIIDAE

Polycentropus cinereus Hagen.—10♂♂, 36♀♀ (ROM) (Fig. 4) June 10—September 5, maxima June 12, August 14, (4, 4 insects). Ross (1944) records this species from Ontario.

Polycentropus (? *interruptus* Banks).—3♀♀ (ROM) Trap 3: August 14—1, August 16—2).

Nyctiophylax vestitus (Hagen).—3 caddisflies (ROM) (Trap 3: June 26—1♂; Trap 4: August 18—1♀, August 25—1♂). Ross (1944) records this

species from Ontario and gives its time of emergence as May to September, a period which includes the dates of emergence from South Walker Pond.

HYDROPSYCHIDAE

Hydropsyche (? *simulans* Ross).—3 caddisflies (ROM) (Trap 2: July 7—1; Trap 5: July 3—1♀, August 13—1♀).

Cheumatopsyche sp. (near *campyla* Ross).—13♀♀ (ROM) (Fig. 4) June 9-August 26.

LEPTOCERIDAE

Oecetis inconspicua (Walker).—4 caddisflies (ROM) (Trap 3: July 28—1♀, July 29—1♀; Trap 4: July 5—1♂, August 7—1♂). Ross (1944) records this species from Ontario and gives its time of emergence as May to October, a

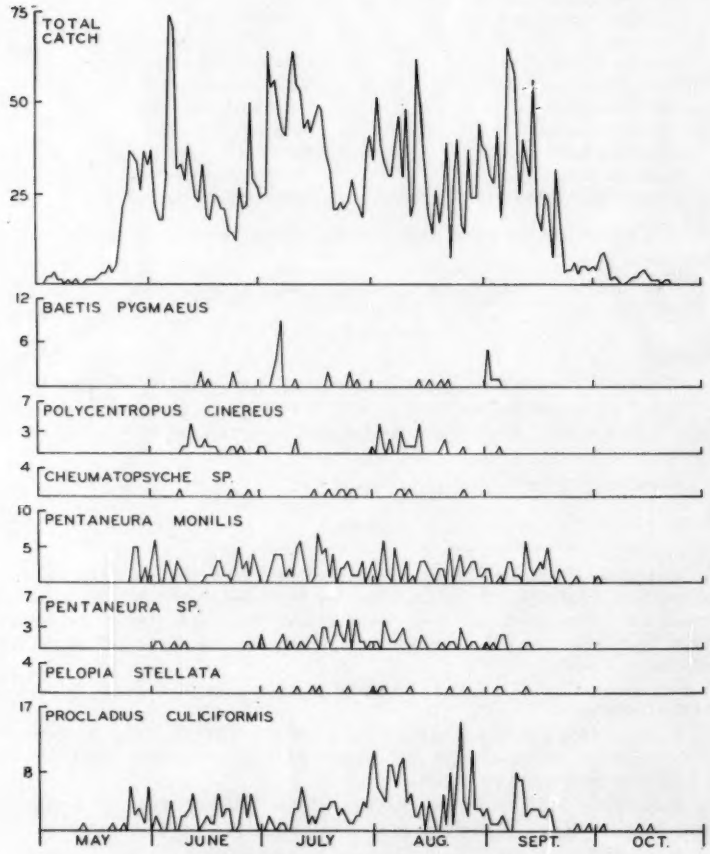

Fig. 4.—Periods of emergence of adult insects.

period which includes the dates of emergence from South Walker Pond.

Oecetis cinerascens (Hagen).—1 caddisfly (ROM) (Trap 4: July 25). Ross (1944) records this species from Ontario.

HEMIPTERA

SALDIDAE

Saldula confluenta (Say).—1 shore bug (USNM) (Trap 4: August 31) This species was previously collected at London by Judd (1957).

MESOVELIIDAE

Mesovelia mulsanti bisignata Uhler.—3 bugs (1, USNM) (Trap 3: September 7—1; Trap 5: August 9—1, August 24—1). This species was previously collected in August at London by Judd (1957).

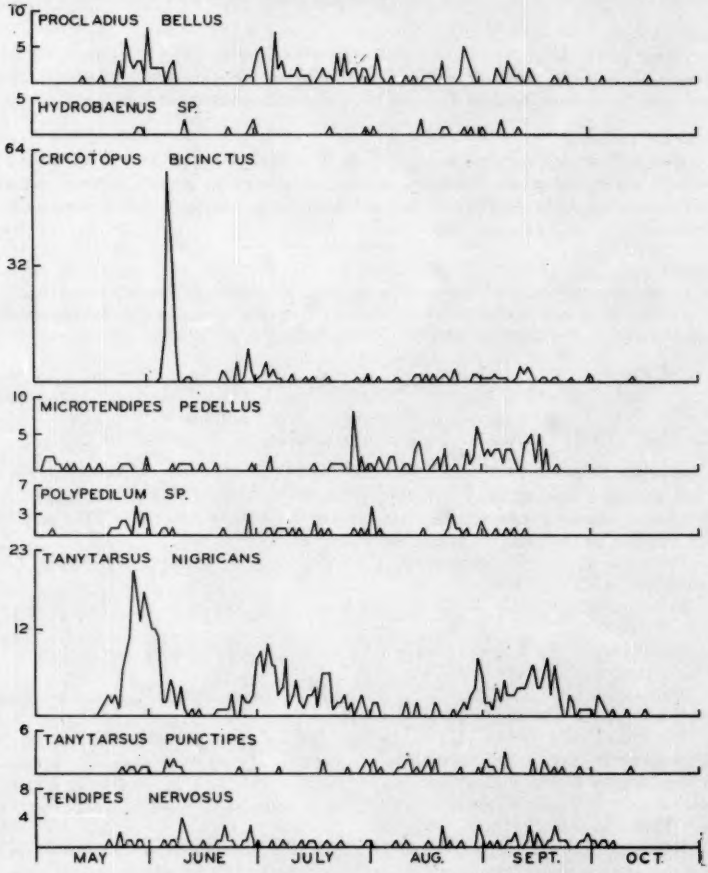

Fig. 5.—Periods of emergence of adult insects.

COLEOPTERA

DASCYLLIDAE

Ectopria sp.—2 beetles (Trap 4: July 8, 17). Blatchley (1910) records that some species of this genus occur in water.

CHRYSOMELIDAE

Longitarsus sp.—1 beetle (Trap 2: August 29). Berg (1949), McGaha (1952) and Usinger *et al.* (1952, 1956) record various chrysomelid beetles as occurring on aquatic vegetation, not including *Longitarsus*. Blatchley (1910) reports that species of *Longitarsus* occur on vegetation.

ANTHICIDAE

Notoxus sp.—1 beetle (Trap 5—July 14). Blatchley (1910) records various species of *Notoxus* as occurring on vegetation about lakes and marshes.

BRUCHIDAE

Bruchus brachialis Fahr.—1 beetle (Trap 1: August 29). Blatchley (1910) records this species from several terrestrial plants. The specimen caught in the trap may have been washed beneath the trap and survived to crawl up into it.

CURCULIONIDAE

Calendra sp.—1 beetle (Trap 4: July 3). McGaha (1952) records several weevils, not in the genus *Calendra*, as feeding on aquatic plants. Usinger *et al.* (1952) record some beetles in the subfamily Calendrinae as being aquatic or semiaquatic.

DIPTERA

TIPULIDAE

Limonia canadensis (Westwood).—1 cranefly (Trap 2: September 11).

Helius flavipes (Macquart).—1 cranefly (Trap 3: August 7). This species was trapped in the Dundas Marsh in Ontario by Judd (1953).

PSYCHODIDAE

Psychoda lativentris Berden.—2 flies (Trap 2: May 30, 31). Johannsen (1934) records several species of *Psychoda* as being aquatic in their larval stage and Judd (1958) records trapping *P. alternata* on the Byron Bog at London.

TENDIPEDIDAE

Pentaneura monilis (L.)—96 ♂ ♂, 135 ♀ ♀ (3, USNM) (Fig. 4) (May 27-October 2, maxima June 2, July 12, August 4 (6, 6, 6 insects). This species was trapped in the Dundas Marsh by Judd (1953).

Pentaneura sp.—80 midges (8, USNM) (Fig. 4) June 2-September 13, maximum July 27 (4 insects).

Pelopia stellata (Coq.)—2 ♂ ♂, 12 ♀ ♀ (1, USNM) (Fig. 4) (July 6- September 12).

Clinotanypus thoracicus (Lw).—1 ♂, 4 ♀ ♀ (4, USNM) (Trap 4: June 23—1 ♂, June 25, 27, July 2, 6—4 ♀ ♀).

Anatopynia dyari (Coq.).—1 ♂ (Trap 1: June 25). This species was trapped by Judd (1957) in June at London.

Procladius culiciformis (L.)—145 ♂ ♂, 218 ♀ ♀ (4, USNM) (Fig. 4) May 18-October 16, maximum August 25 (15 insects). This species was also trapped in the Dundas Marsh and at London by Judd (1953, 1957). In South Walker Pond it occurred above and within the hypolimnion as in Costello Lake, Algonquin Park (Miller, 1941).

P. bellus (L.).—71 ♂ ♂, 73 ♀ ♀ (2, USNM) (Fig. 5) May 15-October 17, maxima June 8, July 7, August 28, (8, 5, 5, insects). This species was trapped also in the Dundas Marsh and at London by Judd (1953, 1957).

Hydrobaenus spp.—21 ♀ ♀ (Fig. 5) May 30-September 12.

Cricotopus bicinctus (Meigen).— 127 ♂ ♂, 94 ♀ ♀ (2, USNM) (Fig. 5) June 1-October 13, maximum June 7 (58 insects). This species was trapped at London by Judd (1957) where the time of maximum emergence was close to that at South Walker Pond. In South Walker Pond these midges emerged mostly from below the thermocline, as was the case in Costello Lake (Miller, 1941).

C. trifasciatus (Panzer).—3 ♀ ♀ (1, USNM) (Trap 1: May 27—1; Trap 3: June 2—1; Trap 5: May 31—1). This species was trapped in the Dundas Marsh by Judd (1953).

Microtendipes pedellus (DeGeer) var. *stygius* Townes.—96 ♂ ♂, 32 ♀ ♀ (2, USNM) (Fig. 5) May 4-September 22, maxima July 27, August 31 (8, 6 insects). This species is recorded from Ontario by Townes (1945).

Polypedilum sp.—34 ♂ ♂, 27 ♀ ♀ (Fig. 5) May 6-September 13.

Tanytarsus nigricans (Joh.) 237 ♂ ♂, 216 ♀ ♀ (2, USNM) (Fig. 5) May 19-October 16, maxima May 28, July 4, September 19 (20, 10, 8 insects). This species was trapped in the Dundas Marsh and at London by Judd (1953, 1957).

T. punctipes (Wied.)—56 ♀ ♀ (4, USNM) (Fig. 5) May 25-October 22.

Tendipes dux (Joh.).—5 ♂ ♂ (2, USNM) (Trap 4: July 7—1, July 10—3, July 12—1). This species was trapped also at London and in the Byron Bog (Judd, 1957, 1958).

T. nervosus (Staeger).—38 ♂ ♂, 47 ♀ ♀ (2, USNM) (Fig. 5) May 21-October 7. This species was trapped also in the Byron Bog (Judd, 1958).

T. riparius (Meigen).—3 ♂ ♂, 3 ♀ ♀ (1, USNM) (Trap 3: August 31—1; Trap 4: July 10, 11, 12, 13, 25—5). This species was trapped also in the Byron Bog (Judd, 1958).

Glyptotendipes lobiferus (Say).—79 ♂ ♂, 51 ♀ ♀ (3, USNM) (Fig. 6) May 19-September 22, maxima June 8, August 30 (9, 6 insects). This species was trapped in the Dundas Marsh and at London by Judd (1953, 1957).

G. brachialis (Coq.).—4 ♂ ♂, 3 ♀ ♀ (2, USNM) (Trap 3: June 29—1, July 6—2, July 23—1, September 4—1, September 13—1, September 29—1). This species was trapped also at London by Judd (1957).

Stenochironomus hilaris (Walker).—39 ♂ ♂, 58 ♀ ♀ (3, USNM) (Fig. 6) June 7-September 6, maximum August 7 (5 insects). This species is recorded from Ontario by Townes (1945).

Calopsectra sp.—468 ♂ ♂, 707 ♀ ♀ (Fig. 6) May 17-October 22, maxima July 10, September 8 (31, 37 insects). These small, green midges were the most common emergents and occurred throughout the season.

HELEIDAE

Atrichopogon sp.—23 midges (10, USNM) (Fig. 6) June 9-September 8, maximum July 4 (4 insects).

Bezzia glabra (Coq.—15 midges (2, USNM) (Fig. 6) June 29-September 9. This species was also trapped in the Dundas Marsh by Judd (1953).

Bezzia sp.—5 midges (USNM) (Trap 2: June 21—1, July 17—1; Trap 3: June 22—1, August 30—1; Trap 4: June 3—1).

Culicoides piliferus R. and H.—5 midges (4, USNM) (Trap 2: June 3, 5, 9—3; Trap 3: June 1—1; Trap 5: June 12—1). This species has been recorded from the United States (Coher) *et al.*, 1955; Lewis, 1959) but not from Canada (Downes, 1956).

Palpomyia slossonae (Coq.).—1 midge (USNM) (Trap 3: June 5).

CULICIDAE

Chaoborus punctipennis (Say).—140 ♂ ♂, 411 ♀ ♀ (Fig. 6) June 8-October 21, maxima June 17, July 11, August 11, September 9 (17, 13, 22, 23 insects).

This species was collected at London and at the Byron Bog by Judd (1957, 1958).

C. flavicans (Meigen).—33♂♂, 40♀♀ (Fig. 6) June 9-September 13, maximum July 12 (12 insects). This species was collected at London and in the Byron Bog by Judd (1957, 1958).

ITONIDIDAE

Itonidini.—Three flies of this tribe emerged in Trap 2 (June 29—2, July 10—1). Johannsen (1934) records that a number of species of gall-flies form galls on aquatic plants.

SCATOPSIDAE

Scatopse fuscipes Meigen.—1 fly (Trap 2: June 29). Johannsen (1934) records rearing larvae of *Scatopse* from an aquatic habitat.

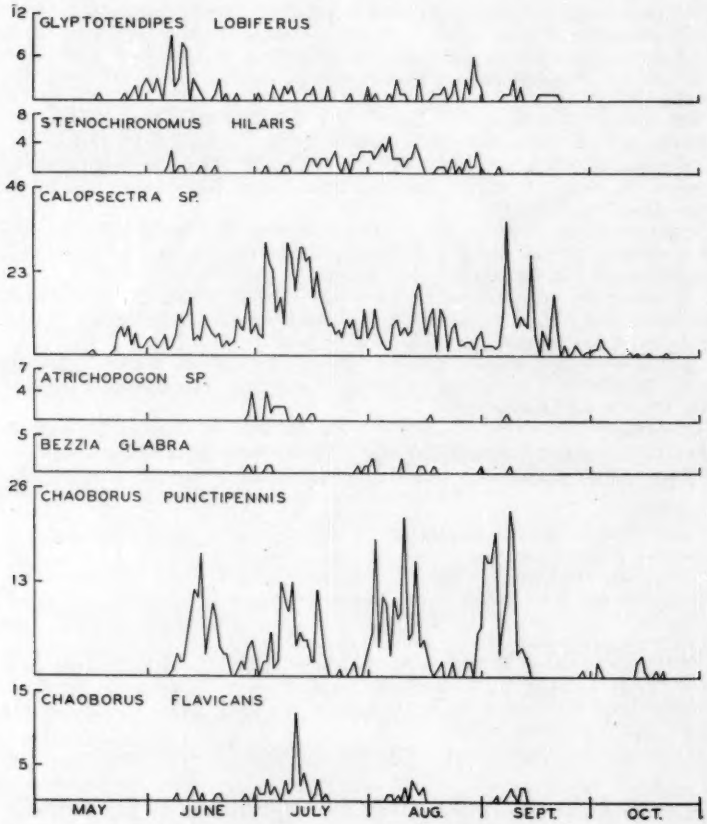

Fig. 6.—Periods of emergence of adult insects.

DOLICHOPODIDAE

Dolichopus sp. (near *monticola* Aldrich).—2 flies (Trap 3: June 17, 22). Several species of *Dolichopus* were trapped in the Dundas Marsh and at London by Judd (1953, 1957).

Tachytrecha sp.—1 fly (Trap: August 27). Usinger *et al.* (1956) record that species of this genus occur along lakes.

EMPIDIDAE

Tachypeza sp.—1 fly (Trap 4: October 8). Usinger *et al.* (1956) list several genera of aquatic Empididae but do not include *Tachypeza*.

EPHYDRIDAE

Hydrellia sp.—5 flies (USNM) (Trap 2: August 21—1, September 6, 12—2; Trap 3: August 31—1; Trap 5: September 8—1).

Scatella picea (Walker).—3 flies (1, USNM) (Trap 3: June 22—2; Trap 5: June 7—1). This species was trapped also in the Dundas Marsh and at London by Judd (1953, 1957).

SPHAEROCERIDAE

Leptocera wheeleri Spuler.—1 fly (USNM) (Trap 5: October 15). Several species of *Leptocera* were trapped in the Dundas Marsh by Judd (1953).

DROSOPHILIDAE

Drosophila melanogaster (Meigen).—1 fly (Trap 4: July 10). *D. quinaria* was trapped in shallow water in the Byron Bog by Judd (1958).

MILICHIIDAE

Desmometopa sordida (Lw.).—1 fly (Trap 4: September 19).

HYMENOPTERA

BRACONIDAE

Apanteles plathypenae Mues.—1 wasp (USNM) (Trap 5: September 10). This species is listed as a parasite of caterpillars (Phalaenidae) by Muesebeck *et al.* (1951). No such caterpillars were collected on the pond but McGaha (1952, 1954) records one species of phalaenid caterpillar which inhabits aquatic plants.

SUMMARY

Between April 10 and November 3, 1956, 4,108 adult insects were trapped in five tent-traps set out on South Walker Pond, two on water over the hypolimnion and three on water not over the hypolimnion. The orders of insects represented were Ephemeroptera (0.99%), Odonata (0.02%), Trichoptera (1.77%), Hemiptera (0.08%), Coleoptera (0.12%), Diptera (97%), and Hymenoptera (0.02%). Midges of the family Tendipedidae constituted 82.5 percent of the Diptera and mosquitoes (Culicidae) 15.8 percent of the Diptera. Other families of Diptera represented were Tipulidae, Psychodidae, Heleidae, Itonididae, Scatopsidae, Dolichopodidae, Empididae, Ephydridae, Sphaeroceridae, Drosophilidae, and Milichiidae. Families of Coleoptera were Dascyllidae, Chrysomelidae, Anthicidae, Bruchidae, and Curculionidae. The numbers and seasonal occurrence, including times of maximum emergence, were recorded for each species. The species were classified according to their relation to the hypolimnion.

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Okinawa's Dry Typhoons[1]

JACK C. ELLIOTT[2] AND YOSHIMA NINO[3]

Tropical storms of typhoon and near typhoon intensities long have been a part of the climatic variabilities of the Ryukyu Islands. Such storms have had a harassing influence on the lives of the people as they have endeavored to wrest a living from the land, keep their homes intact, and fish the in-shore waters. A forty-year summary of climatological records from the Ryukyuan Weather Bureau (1956) indicates that the islands are usually visited by typhoons each year. Most frequently a minimum of three tropical storms, with wind velocities of 65 miles per hour or more, plague the islands each summer. Some years there have been more, some years there have been less, and it is an atypical year when at least one tropical storm of typhoon intensity is not recorded by the Weather Bureau and its effects felt by the people. According to these records typhoons have blown over the Ryukyus every month of the year; however, the usual season is from late July until early October, during the hot, dry period.

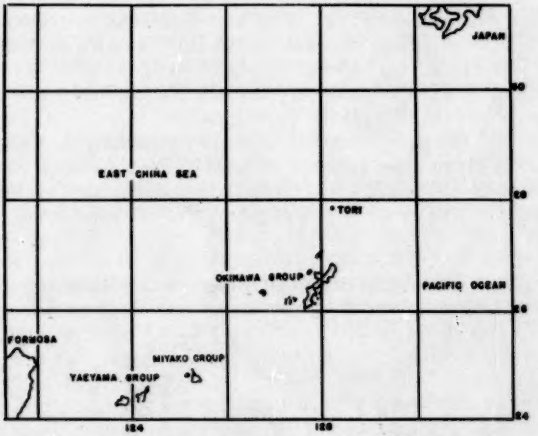

Fig. 1.—The Ryukyu Islands under control of the United States Civil Administration.

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LOCATION, AREA, POPULATION

The Ryukyuan Archipelago, composed of numerous islands, islets, and exposed coral reefs, extends nearly 750 miles in a north-easternly direction from a point northeast of Taiwan (Formosa) to near the southern islands of Japan. Yaeyama Gunto (Group), the southernmost one, is just north of latitude 24° N., and the northern-most one, Tori, slightly south of latitude 28° N. The western edge of the island chain is marked by longitude 123° E., the eastern by longitude 132° E. Thus to the west of the major island group is the East China Sea, and to the east the Pacific Ocean (Fig. 1).

Okinawa, the largest island of the chain, covers 64 percent of the total land area. Its southern tip, (Kiyonsaki) is 26°, 5′ N. latitude; north cape (Hedo-saki) 26° 52′ N. latitude, and the 128° meridian of longitude E., passes through the north-central portion.

According to a 1955 population census (United States Civil Administration, 1956) there were 680,905 people living on Okinawa. This figure represents 85 percent of the total population of the Ryukyus. The economy of the island is agricultural, with 55 percent of the total labor force so employed.

1956 TYPHOON SEASON

During the summer of 1956 five typhoons struck the Ryukyu Islands (Table I). Four of these storms hit Okinawa directly, whereas the fifth lashed the island with winds of near typhoon intensity. Although damage to man-made objects was considerable, this paper will discuss only effects of typhoon on vegetation.

Wind and salt-spray damage from the typhoons retarded maturation of most crops, and resulted in near failure in a few instances. Two typhoons ("Wanda" and "Harriet") were "dry" (those during which there is little or no precipitation), and caused considerably more

TABLE I.—Typhoons affecting Okinawa during the 1956 season

Name of Typhoon	Period Typhoon Within Area of Approximately 240-Mile Radius with Center at Naha				Wind Velocity Recorded at Naha (Miles Per Hour)		Approximate Total Precipitation at Naha During Typhoon Period (Inches)
	Entered		Departed			Maximum (Gusts)	
	Date	Time	Date	Time	Average		
Wanda	7/31	0200	8/1	1900	73	111	8.0
Babs	8/14	1000	8/16	1400	64	94	7.4
Diana	9/1	1100	—	—	35	52	0.32
Emma	9/7	1200	9/9	1100	97	165	15.2
Harriet	9/25	2400	9/26	1800	87	129	3.96

salt-spray burning to crops and natural vegetation than intervening ones, which coincided with considerable rainfall. Although data in Table I are indicative of heavy rains during "Wanda" and "Harriet," a factor not revealed by these data is that rains did not come until the waning hours of the storms, which was too late to wash off wind-blown salt-spray before considerable burning had taken place.

EFFECT ON NATURAL VEGETATION

The zonation of vegetation along the coastal areas, and the effect of salt-spray on that vegetation has held the interest of numerous investigators for many years. Boyce (1954), in reporting the results of an intensive study of the "Salt Spray Community" has reviewed the extensive literature on this subject. In most instances these investigations were carried on in coastal regions where the vegetation has been subjected to long periods of salt-spray depositions and thus reflects the results of actions and reactions over a long time span.

Similar results may be seen reflected in the zonation of coastal vegetation on Okinawa. Ryukyuan Pine (*Pinus luchuensis* Mayr.)[1], common along the coast and on high headlands, is quite asymmetrical, with contorted top, short seaward-side limbs, and long, graceful, landward-side branches (to many a U. S. Serviceman, remindful of the Monterey Pine). Numerous "Shrine forests," composed of pure stands of Sea Hearse (*Hernandia sonora* L.) growing on sandy strand or rocky beach, have a graded stature in both height and girth from strand landwards; those nearest the sea are much misshapen with a definitely asymmetrical growth habit. In the scrub forests located near the sea, the velvet-leaf tree (*Messerschmidia argentea* (L.) Johnst.), which usually has the greatest abundance nearest the shore line, likewise shows the effects of nearly continuous salt-spray depositions by a growth habit peculiar to its ecological niche. Other members of this community which respond in a similar way are Orange Jessamine (*Murraya paniculata* (L.) Jack.), *Macaranga tanarius* (L.) Muell., *Premna obtusifolia* R. Br. and several species of fig (*Ficus*).

However, certain environmental differences are present under typhoon conditions which act and react to produce results that are varied from those produced under normal coastal situations. Noticeable among these differences are: 1) deposition of a high salt concentration over the entire plant body, rather than on the windward side only; 2) the relatively short length of time that these plants are subjected to these critical conditions; 3) the exceedingly high wind velocities, often producing mechanical injury, thus allowing easy entrance of salt solutions. In the first instance a heavy salt concentration quickly covers the aerial portion of the plant. Plasmolytic reactions occur throughout the whole plant body, rather than the more common one-sided reactions produced within coastal environments. Secondly, the

[1] Nomenclature is that of Sonohara, Sakuya; Shinjun Tawada and Tetsuo Amano. Flora of Okinawa. 1952.

length of time that the plants are subjected to these conditions is variable. Many typhoons are accompanied by heavy rains which serve to wash much of the salt-spray from the plant before severe burning can result. This factor may account, in part, for their speed of recovery if mechanical injuries have not been too extensive. In Okinawa, however, "dry" typhoons are not infrequent. In such instances considerable burning of the vegetation is common and the results are most spectacular, yet devastating. In the third place, the extremely high winds serve to increase and accelerate processes of mechanical injury, thus allowing greater infiltration of salt solutions. These factors combine to produce noticeable dwarfing of the whole plant. Along the coast, where the vegetation is subjected to salt-spray almost continuously, the asymmetrical growth habit is accompanied by dwarfness as result of the influence of many past typhoons.

FORESTED AREAS

The topography of the north-central portion of the island is undulating to hilly, interspersed with broad valleys and small, flat plateaus. Most of the soil of the area is deep, rapidly drained, high in acidity, steep and nonarable. This part of Okinawa, not utilized for agricultural purposes, villages, or U. S. military installations, has a fine stand of young Ryukyuan pine. Strong typhoon winds produced little breakage of limbs, tops, or wind-throw. Gales, however, increased transpiration rates sufficiently to produce some "transpiration burn" with a consequent set-back to developing young shoots. Heavy salt burn (distinguished from "transpiration burn" by complete yellowing of needle-leaves) was a conspicuous feature within the area, with needle-leaves, limbs, and bark showing injury. Some sand-blasting of bark from lower parts of trunks likewise occurred. Numerous mis-shapen trees are certain to result from the effect of these typhoons and susceptibility to diseases will be noticeably increased because of bark injury. Cone and seed production was markedly reduced. Young cones were burned beyond recovery and older, but immature ones were blown from the trees. A high percentage of young seedlings, too short and supple to be much affected by the winds, were killed as a result of salt depositions from the "dry typhoons."

Farther to the north, in the mountainous areas of the islands, the pines are mostly confined to the lower third of the generally steep slopes. Protection afforded by the precipitous areas above the pine zone kept typhoon damage to a minimum, especially within the interior. Stands along the coastal slopes on both the Pacific Ocean and East China Sea were affected in much the same manner as described above. However, that typhoons can do strange things on occasion may be seen from the fact that some of the most severely burned pines were found in what appeared to be well-protected, interior valleys, with no indication from the vegetation around them to suggest probable pathways of approach.

Much of the mountainous area of northern Okinawa supports a broad-leaved, evergreen forest; the "Lauri-silvae" of the Japanese (Walker 1952-1954). During the early years of World War II, the Japanese effected a heavy timber-drain on the area for naval supplies. At the conclusion of the war, the area again was the scene of much lumbering activity in order to supply construction materials for post-war building. Consequently, today, the stands are mostly of coppice development, numerous in stems, small in stature, and frequently much contorted in shape. Large trees are mostly culls, either left from former lumbering operations, or confined to nonaccessible areas. Abundant in this community are "Iju" (*Schima liukiuensis* Nakai) and "Okinawa-shii" (Okinawa chestnut) (*Castanopsis cuspidata* (Thunb.) Schottky) with an admixture of numerous members of the Lauraceae, Ebenaceae, and a lesser representation of other families.

Wind-throw was most evident among the larger and older trees after the passing of the typhoon. Damage to young, immature fruits from limb-rub and wind-whip was common, seriously reducing the year's seed crop. (For example: A seed exchange which had been arranged with the Forestry and Timber Bureau, Commonwealth of Australia for *Schima* had to be postponed until another growing season). Burn from salt-spray was prominent, causing defoliation, as well as death to new growth on the trees. Although regions evidencing greatest injury were generally to be found along the coast, and in coast-facing river valleys, areas of like damage were apparent on the highest mountain (Mount Onna, 636 meters) as well as in some interior depressions, indicating that wind-blown salt-spray was carried completely across the island.

On frequent occasions, especially following the "dry" typhoons, woody species were seen to renew their reproductive cycles following defoliation. The phenomenon appeared most frequent among members of the Moraceae, with individuals of *Morus australis* Poir., for instance, putting forth new catkins and leaves following three "dry" typhoons, before finally succumbing to the vicissitudes of subsequent storms.

Upsets in the life-cycles of vegetation, whether frequent, as is apparently the case in Okinawa because of the effects of numerous typhoons, or seldom, as might be induced by infrequent, catastrophic storms or man's disturbance, are important ecological elements which need to be considered when analyzing the vegetation in any region. This factor is of considerable magnitude when synecological investigations, aute-ecological studies of native species, and planning programs for introduction of new species on Okinawa (or elsewhere) are considered. Costello (1957) has pointed out that: "Disturbances in life cycles are the causes of change in range conditions and productivity, and therefore, the source of many problems in range management." So, also, are they potential sources of problems when not adequately considered as a part of the total ecology of an area.

WILD ("GENYA") LANDS

Nonarable land in the central and southern portion of the island is called "Genya" (Wild) land by the Okinawans. Composed of thin-soiled, steep hills, with local limestone outcrops, it makes up 40 to 45 percent of the area. The principal components of the wild-land vegetation are grasses, especially *Miscanthus floridulus* (Labill.) Warb.; vines, (*Vitis sp., Smilax sp.*); shrub thickets, (*Rosa bracteata* Wendl., *Rubus grayanus* Maxim., *R. sieboldii* Blume., *Rhaphiolepis umbellata* (Thunb.) Makino., *Pittosporum denudatum* Nakai., *Leucaena glauca* (L.) Benth. and in some instances communities of Cycad (*Cycas revoluta* Thunb.), Ryukyuan Pine and small-leaved banyan.

The extensive areas of Sword-grass (*Miscanthus*) are the main source of supply for thatching materials and for the cottage industry of "Panama" hat manufacture. They are, therefore, of considerable importance. Cycad ("Sotetsu") leaves are used for decoration during festivals and celebrations, and the fruits are utilized on occasion of severe food shortage. Most serious damage to the vegetation of the wild-land occurred to the shrub aspect where fruits, used as a part of the diet, were badly bruised from limb-rub and wind-whip, and blown-off, or withered as a result of salt-spray deposition. Considerable defoliation also was produced. Nearly pure stands of "Gingokan" (*Leucaena glauca* (L.) Benth.), a source of charcoal stock and kindling wood, stood gaunt and bare after the effects of the "dry" typhoons and it was several months before new growth became evident. Although there was some browning of leaf and stem, the vegetative portion of the grasses was slightly damaged from salt burning. Flowering, however, was considerably affected, with as much as 70 percent of the area failing to produce the "silver plume" so characteristic of *Miscanthus* during October and November.

The influence of typhoon damage on the vegetation of wild ("Genya") lands is difficult to evaluate. Certainly some loss to the wild fruit crop has much reaction on the supplementary diets, and the beating taken by "Gingokan" prevents it maturing into a very sizeable tree or shrub for firewood or charcoal-stock. Whereas, the vegetative portion of sword grass is little damaged, the loss of flowering and fruiting stages reduces to some degree the extent of new areas for thatching materials. According to Okinawan botanists (Shinjun Tawada, Forestry Section, Department of Natural Resources, Government of the Ryukyuan Islands, and Professor Shunichi Shimabukuro, Dean, Agriculture and Home Economics Division, University of The Ryukyus) the grass aspect of the wild-lands was dominated by Cogon (*Imperata cylindrica* (L.) Beauv.) previous to the war; the establishment of sword grass (*Miscanthus floridulus*) was an aftermath of the devastation which occurred to the central and southern portions of Okinawa. Peculiarities of the edaphic situation would appear to be an important factor in determining the unique nature of the "Genya" land's vegetation. Typhoons have, no doubt, exerted

some influence and selective action, and the prewar abundance of Cogan grass could be related to its apparent typhoon resistance. The long-time influence of man, as well as his more recent greater destruction through war activities, must be acknowledged. Thus it is possible that the present vegetational aspect of the "Genya" lands is, to a greater or lesser degree, one of a successional nature.

EFFECT ON CROPS

Sweet potatoes.—This crop, which occupies the largest planted area of the island and serves as the basic food, was damaged to the greatest extent. Plantings normally made in early July but delayed because of hot, dry weather, were badly burned from the effects of the "dry" typhoon "Wanda," and rendered almost a complete loss by "Babs," two weeks later. Efforts to replant were continued through the arrival of "Harriet" with little success. Thus, three months of the usual growing season were lost to crop production. Numerous plots, established on beach strand, were covered with 3-5 inches of wind-driven sand causing further loss to the total annual production.

At the present time three varieties of sweet potatoes are grown most extensively on Okinawa: Okinawa No. 1, Hijagawa No. 1, and Yaeyama-akago. These varieties are the result of a breeding program carried on by Yogi Agricultural Experiment Station (Government of Ryukyu Islands Institution) since prewar days. Previous to the war, all sweet potato breeding for Japan was carried on by this station as these plants bloom in Okinawa and therefore do not require crossing with Morning Glory (Kohler, 1957). Whereas these varieties are relatively resistant to diseases common to the islands, they all require a six-month growing season, and difficulties can be encountered when the planting time coincides with a typhoon season, as frequently happens. Efforts to secure a suitable stock requiring a shorter growing period are being put forth by the Agricultural Division, University of The Ryukyus and Yogi Experiment Station through importation of likely varieties from other countries. Some success has been obtained with varieties from the state of Louisiana (U.S.A.); however, experiments have not yet reached a stage where plants can be released in abundance to growers. Real promise for a solution to this problem lies in a plant breeding program, still in its early stages, at the several Ryukyuan Government stations and at the University of The Ryukyus. Taking into account the ecological concept of day-length and photoperiodicity, experiments are being conducted in an effort to breed a disease-resistant, high yielding variety, requiring a growing season less than the present six-month one. Success in this program would do much to offset the serious losses experienced with this crop in years of numerous "dry" typhoons; as Nuttonson (1952) has said, "The Ryukyus, already suffering a chronic food deficit, could ill afford to sustain major damage to the sweet potato crop."

Sugar cane.—Greatest damage to this, Okinawa's most important export crop, was from the effects of high wind velocities rather than from burning by salt-spray. Fields of young cane planted in April or July had their foliage leaves and growing points severely damaged with each successive typhoon. In numerous instances, the leaves were completely stripped from the stem, in other situations they were badly torn and shredded, necessitating regeneration with the onset of favorable growing conditions. In plots of older cane, planted the previous year, stalks were blown nearly flat and several weeks were required before they assumed an upright position. Thus, with tillering and lodging of the mature cane, and processes of regeneration necessary in the younger stands, the usual harvest dates were delayed by more than a month. Fortunately the cane could be harvested by the use of the customary hand-sickle, whereas the lodged cane could not have been harvested by mechanical means.

Because of the severity of damage to the cane, the 1956 yields did not exceed those of the 1955 season despite the fact that the 1956 cane acreage had been increased by 20 percent. Further losses to the crop, as a result of typhoon damage, are indicated in harvest reports from the several contrifugal sugar mills. These reports indicate an increase in fiber-content, whereas measured sugar-content decreased from 18 or 19 degrees to 14 or 15 degrees (Kohler, 1957). August and September plantings were delayed because of bad weather and overly wet soils created by the typhoons and their accompanying rains.

Rice.—Typhoon damage to paddy-lands, seed-beds and transplants, which were being readied for the second annual rice crop, resulted in approximately a 20 percent loss when compared with yields of previous years. Most extensive damage came when man-made sea-walls were breached by the surf, thereby permitting inundation, erosion, and sedimentation of paddy-lands. Heavily sedimented areas required reclamation measures before return to cultivation. Most seed-beds were planted following typhoon "Wanda," with transplanting taking place after the passing of "Babs." Heavy rains accompanying the later typhoon flooded many of the seed-beds resulting in suffocation of the plants before the excessive water could be drained off. Additional losses occurred as the result of more suffocation and erosive action during and immediately after typhoon "Emma." Dry "Harriet," the last typhoon of the season, produced some burning. This effect was most evident in narrow valley bottoms along the west coast in the southern part of the island. Here, apparently, narrow valleys, running at right angles to the coast, served as funnels for the winds with their heavy loads of salt-spray. Consequently the upper third of the rice plants in paddy-lands so situated were considerably burned. Inspection of the areas, two weeks after the incident, showed almost complete recovery, however.

Papaya and banana.—There was no crop of papaya (*Carica papaya* L.) fruits on Okinawa in 1956. "Dry" typhoon "Wanda," with

high wind velocities and heavily laden with salt-spray, came upon the plants as the fruits were starting to set, or were in early stages of maturation. Plants not broken off by the typhoon were left standing apparently lifeless; foliage leaves burned and withered, and fruits dangled as dry, shrunken, brown balls. No evidence of renewed growth was apparent in the two weeks elapsing between "Wanda" and "Babs." By September, when "Emma" blew in, new crowns of foliage leaves were beginning to appear. Following "Emma," those plants still standing remained slim, stark, pillars until a flush of new growth started to show during late March and early April, 1957.

Fiber banana plants (*Musa liukiuensis* (Matsum.) Makino.) with their massive, pendant leaves, were blown down, or leaves so badly shredded as to render them useless for the cottage textile industry. Only in a few isolated instances, in deep well protected valleys in northern Okinawa, were these plants spared destruction. The edible banana (*Musa paradisiaca subsp. sapientum* (L.) Kuntz.), a frequent court-yard plant grown for family consumption, suffered a similar fate.

Pineapple.—Although there was little apparent direct damage to pineapple from the typhoons, there was, nevertheless, considerable soil erosion when rains beat down on recently established plots, and rivulets gullied through them from higher areas. Extensive growing of pineapple is comparatively recent in Okinawa (12 acres in 1952, 400 acres in 1956). It is planted on bench-terraced hillsides where formerly grasses, shrubs, and second-growth sprout forests served to prevent serious erosion. Improved terracing methods, with careful thought given to contour shape, are urgently needed, if this phase of Okinawan agriculture is to develop into a long-time, profitable practice.

Commercial gardens.—Growing of fresh vegetables for Quartermaster and wholesale-retail sales has become an important part of the farming activity in the past several years. Because the hot, dry summer months are the "off-season" for this truck-crop, relatively little total loss was experienced. Some damage, however, occurred to the late, unharvested tomatoes, squash, melons, cut-flower stock, etc. Burning from the salt-sprays of "dry Wanda" was a prime factor in the latter instance.

Home gardens.—Decorative plantings around the government buildings, school houses, and the concrete, typhoon resistant homes in the several American Dependent housing areas were greatly affected by typhoon damage. The shrubs: Hibiscus (*Hibiscus rosa-sinensis* L.; *H. syriacus* L.; *H. schizopetalus* (Mast.) Hook, f.; *H. mutabilis* L.); Japanese Privet (*Ligustrum japonicum* Thunb.); Crepe-Myrtle (*Lagerstroemia indica* L.); Seven-colors (*Lantana camara* L.); several species of Bougainvillea (*Bougainvillea spectabilis* Willd., *B. spectabilis var. lateritia* Lam., *B. glabra* Choisy); Blood-flower Milkweed (*Asclepias curassavica* L.) and others were nearly defoliated and their grow-

ing tips badly burned during "dry Wanda." New leaves appeared within a week to ten days; however, the effect of lashing winds and driving rains during later typhoons kept them in a state of retarded growth until several months after the final storm of the season. Broadleaf evergreen trees: Acacia (*Acacia confusa* Merr.); Coral Tree (*Erythrina variegata var. orientalis* (L.) Merr.); Rosewood (Autumn Maple) (*Bischofia javanica* Blume.); Small-leaved Banyan (*Ficus retusa var. nitida* (Thunb.) King.), used as yard plantings were severely injured. Defoliation and killing of tender, new twigs from salt-spray burn of the first typhoon set the growth of these trees back to such an extent that some failed to recover; others were only starting to show signs of renewed life in December. The needle-leaved trees; Ryukyuan Pine and Australian Pine (*Casuarina equisetifolia* J. & G. Frost) were likewise badly burned from salt-spray and there was considerable deformation from top and limb breaking among the latter species. Vines used for shade and concealment were injured in various ways. Most affected were Morning Glory (*Ipomoea purpurea* Lam.) and *Wisteria floribunda* (Willd.) DC. Flower beds of annuals, biennials and perennials were either burned beyond recovery or washed out by torrential rains, necessitating new plantings with the advent of suitable growing conditions.

Windbreaks.—Effective tree and shrub windbreaks are an important adjunct to Okinawan life. Species must be used which can withstand not only the many typhoons, but also the year-around, more or less steady monsoonal winds as well. Nuttonson (1952) has pointed out that wind velocities of 38 miles an hour or more have been recorded in every month of the year on the island.

Windbreaks for protection to agricultural crops are used most extensively along coastal flats, valley entrances, and on the higher plateaus. Screw-pine (*Pandanus tectorius var. liukiuensis* Warb.) is most commonly used along the coastal flats where it serves the dual purpose of windbreak and sand-binder. Frequently, one or more rows of Australian Pine are planted on the cultivated side of the Screw-Pine in order to give additional height to the windbreak. Australian Pine, along with Alexandrian Laurel (*Calophyllum inophyllum* L.) and Garcinia (*Garcinia spicata* Hook.f.) are more frequent in the other two situations, with the former being the most common. A species of rapid growth, Australian Pine was introduced following the war to replace windbreaks then completely wiped out.

Domestic windbreaks are used around rural homes, villages and towns for protection from winds and to lend some degree of privacy to the open-type dwellings. Tall hedges of Hibiscus (*Hibiscus rosa-sinensis* L.) with groves of Alexandrian Laurel, *Garcinia,* and Australian Pine constitute the more common type. On occasion small and large-leaved banyans (*Ficus retusa var. nitida* (Thunb.) King - *F. superba var. japonica* Miq.) may be found interspersed with the other species. Walker (1952-1954) has described the appearance of these domestic windbreaks as follows: "Most striking among the cultivated

trees in every village is the 'fukugi,' *Garcinia spicata,* a dark-green, thick-leaved introduction from southern Asia, its shape reminding westerners of the lombardy popular. It grows in close rows along the streets and property lines, and, because of its slow growth, one can guess from the size of the 'fukugi' trees the age of the village."

These windbreaks withstood the high wind velocities of the typhoons and their accompanying salt-spray with varying degrees of success. Most resistant was Fukugi. There was little or no breaking of trunk or limbs, and although leaves were badly browned from salt-spray burn, no defoliation occurred. Alexandrian Laurel likewise withstood the storms well, having a minimum of breakage and some defoliation in areas nearest the coast. Australian Pine suffered the most damage, both from high wind velocities and burn from salt-spray. Most of these trees had their young branches killed from the effects of salt depositions and in many instances the upper third of the crown was blown away. Rows of Australian Pine, which before the storms were forty feet or more tall, resembled tall hedges following trimming operations necessary to remove broken tops, side branches and dead portions. Some typhoon damage to Screw-pine windbreaks was evident following the passing of "Emma," the third storm of the year, when they began to look beaten and gray. It is possible, however, that some of this appearance resulted from a picking of fruits and leaves for use as offerings at ancestral tombs during the mid-September Oban ceremony. Hedges of Hibiscus, defoliated during "Wanda" remained naked and gaunt for the remainder of the typhoon season.

Because of the extensive damage to Australian Pine from the typhoons it is apparent that it will be necessary to re-evaluate the use of this species as a common windbreak tree. Whereas resistance to salt-spray burn and wind breakage make *Garcinia* and Alexandrian Laurel desirable species, their slow growth rate reduces their value in early stages of windbreak establishment. Until such time as a satisfactory replacement can be found for Australian Pine it may be feasible to combine Screw-pine with *Garcinia* and Alexandrian Laurel thereby getting some protection from Screw-pine during the period that the other two species are growing large enough to offer protection from the winds.

There is one bright spot, floristically speaking, on the "typhoon horizon" of Okinawa. Thirty-six to forty-eight hours after the passing of a storm, Typhoon (Zephyr) Lilies, — pink (*Zephyranthes grandiflora* Lindl.) and white (*Z. candida* Herb.) —, burst into bloom. Used extensively along approach walks or bed-borders, they are the one bright spot of color in an otherwise black-burned, wind-whipped vegetation, and they seem to beckon to a discouraged people as if to say, take hope, there is yet life in the plants.

SUMMARY

"Dry" typhoons on Okinawa have a deterrent and upsetting effect

on the life cycles of its vegetation. Heavy salt depositions from spray blown from surrounding salt waters serve to: 1) destroy tender growing points, retarding growth; 2) cause considerable defoliation, thus upsetting normal food metabolism processes; 3) set-back formation and development of reproductive processes, reducing supplies of fruits and seeds; and 4) produce an added aspect of asymmetrical growth-form and dwarfness to coastal vegetation. High wind velocities cause damaging effects by: 1) bole and limb breakage; 2) windthrow; 3) wind-whip and limb-rub to fruits; and, 4) transpiration burn, which affects plant-water balances. Typhoons which are not "dry" create the same effects as regards damage from high velocities. In some instances salt burn occurs when the rains do not come in early stages of a typhoon. Typhoons accompanied by torrential rains increase erosion processes and most frequently result in damaging floods to paddy-land and other farming areas.

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Differentiation and Commensalism in Podocoryne carnea[1]

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Podocoryne carnea is a commensal hydroid which attaches as a planula to the shell of a hermit crab. Here the planula metamorphoses into the mature hydranth form, and a colony is produced asexually by means of stolons which grow from the base of the hydranth (Fig. 1). More hydranths develop upon the stolons. Ultimately a colony consisting of three major types of hydranths exists on the hermit crab shell: (1) nutritive hydranths, the feeders, resembling pond hydra; (2) generative hydranths, producing medusae which in turn liberate

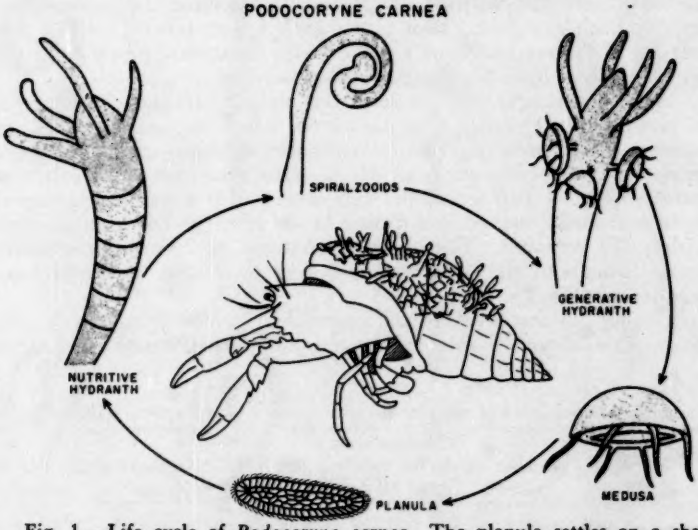

Fig. 1.—Life cycle of *Podocoryne carnea.* The planula settles on a shell occupied by a hermit crab and metamorphoses into a nutritive hydranth. From the base of the hydranth stolons grow, and upon the stolons other hydranths form. Mature, crab borne colonies have a hydranth population consisting of nutritives, generatives, and spiral zooids. Generative hydranths form and release medusae which swim about and discharge gametes into the water. The gametes unite and give rise to the planulae.

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gametes; and (3) the spiral zooid, an elongate, filiform hydranth, coiled like a watch spring, which responds to stimulation by a violent uncoiling. It is the commensal nature of spiral zooid genesis with which we are here concerned.

Although colonies can be maintained in the laboratory by transplanting single hydranths to microscope slides, it is notable that only the nutritive and generative hydranths will differentiate on these colonies. The spiral zooid never forms on slide-grown colonies. Also of interest is the fact that on the crab shell spiral zooids appear only around the opening from which the crab emerges. On the basis of these two observations, one may assume that the crab is in some way responsible for the differentiation of spiral zooids. Such an assumption is easily tested. The results, detailed in Table I, substantiate this hypothesis.

Hermit crabs (*Pagurus longicarpus*) were removed from *Nassa trivittata* shells bearing *Podocoryne* colonies by treating the crabs with sea water through which CO_2 had been bubbled.

To one group of shells, maintained as controls, crabs were returned. The other shells, without crabs, comprised the experimental group. Each group was kept in a 4-inch finger bowl partially submerged in the sea table and supplied with constantly running sea water which had been filtered through glass wool.

After 6 days, spiral zooids remained on only one shell in the group of non-inhabited shells. Five days later, when no spiral zooids remained, crabs were returned to a number of these shells. Within 5 more days, all of the shells to which crabs were returned exhibited spiral zooids. Repetition of the experiment with a different group of crabs and shells resulted in a similar loss of spiral zooids from all shells with crabs removed. The shells maintained as controls, containing crabs throughout the experiment, showed no change in spiral zooid population (Fig. 2).

During the first week of the experiment, while spiral zooids were disappearing from the colonies, these zooids were observed in all stages

TABLE I.—Dependence of spiral zooid maintenance on a *Pagurus* supplied factor

	Number of colonies	Colonies with spiral zooids after 10 days		Number of colonies	Spiral zooids reappeared
EXPERIMENT 1					
Crabs removed	29	0	crabs returned	24	24
			crabs not returned	5	0
Crabs present	16	16			
EXPERIMENT 2					
Crabs removed	27	3	Time limitation prevented further verification of the ability of these colonies to form spiral zoooids when crabs are returned.		
Crabs present	6	6			

of their transformation to either nutritive or generative hydranths. The details of this transformation will be reported separately.

Some idea of the nature of the crab's influence upon this differentiation may be gained from the fact that after spiral zooids had disappeared from the colonies, a new type of zooid was seen to arise. This was a small hydranth, devoid of tentacles, with a band of orange pigment proximal to its rounded end. No hypostome could be observed at this end. Within 24 hours of their appearance, such hydranths formed tentacles, and within 3 or 4 days they could not be distinguished from nutritive hydranths. Nutritive hydranths normally display tentacles almost immediately after the hydranths appear as slight swellings on the stolon. This phenomenon would seem to indicate that although colony differentiation is responsible for the appearance of a specialized hydranth type, the crab supplies some factor necessary to spiral zooid maintenance and to subsequent differentiation.

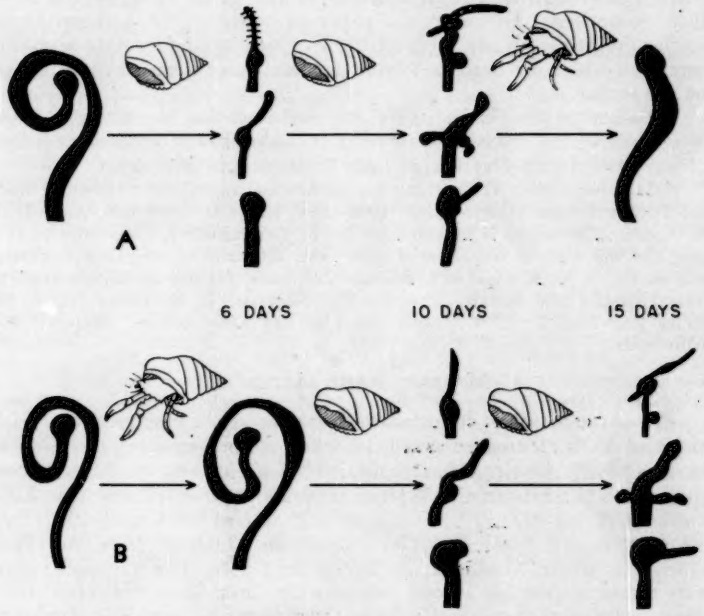

Fig. 2.—Normal and experimental production of spiral zooids. A. — The transformation of spiral zooids on shells from which the crab had been removed. After ten days without the crab, tentacles grow from the end of the hydranth, or else the distal portion of the spiral zooid thins to form a tentacle; medusa buds grow from more proximal portions. Within five days after the crab is returned to the shell small spiral zooids appear. B. — A control experiment run simultaneously with that shown in A. Spiral zooid maintenance continued only so long as the crab was in the shell.

Studies on Virgulate Xiphidiocercariae from Indiana and Michigan[1]

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The Cercariae virgulae was proposed by Lühe (1909) to include five species of xiphidiocercariae containing a pear shaped "organ" in the oral sucker. Since that time, approximately 50 additional species belonging to this group have been described, and in seven instances they have been shown to be larvae of the trematode family Lecithodendriidae. Many of these cercariae have been described so incompletely that if found again their identification would be a matter of conjecture. For that reason a review of the entire group would be of little value here. However, the paper of Seitner (1945) is significant to the present study, as three of the five species of virgulate xiphidiocercariae which he described from Indiana have been studied further by the writer.

Another paper (Hall, 1959) has reported the life history of one of the three; the remaining two are included below with descriptions of ten new virgulate cercariae from Indiana and Michigan.

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Materials and Methods

Prosobranch snails collected and examined for emerging cercariae included 5595 *Pleurocera acuta,* 1831 *Goniobasis livescens,* 467 *Goniobasis* sp., 3953 *Amnicola limosa,* and 680 *Campeloma* sp. Most of the snails were taken from the Wabash and Tippecanoe Rivers near Lafayette, Indiana during the summer and fall of 1956 and 1957, but the unidentified species of *Goniobasis* was obtained from the Pere Marquette River, Michigan, in September, 1956. The various arthropods tested as possible second intermediate hosts were collected from these rivers and from Little Pine Creek near Green Hill, Indiana, where no snails harboring virgulate cercariae could be found. Arthropods were placed with freshly emerged cercariae for 2 to 24 hours, the period of exposure depending on the number of cercariae available.

[1] Based on part of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Purdue University, August, 1958.

Cercariae were studied alive and after fixation in hot 3 percent formalin as described elsewhere (Hall, 1959). Measurements are in millimeters and are from specimens fixed in formalin after natural emergence from the snail. Drawings are free hand and to scale from numerous measurements; those of entire, fully developed cercariae are based on formalin fixed material, while those of developing cercariae, sporocysts, and metacercariae are from living material.

OBSERVATIONS

Specific characters of virgulate cercariae include the length and shape of the stylet; size and shape of the virgula organ; position, texture, and staining reactions of the cephalic glands; the arrangement of their ducts; the shape of the excretory bladder; and the flame cell pattern. The following general diagnosis applies to all of the species considered below and is given to avoid repetition of characters which they have in common:

Small distome cercariae, ventral sucker smaller than oral sucker, mouth subterminal. Oral sucker with virgula organ consisting of a pair of sacs containing a homogeneous mucoid substance; sacs fused or not posteriorly and opening within oral sucker near mouth. Stylet set horizontally in oral sucker, with more or less distinct shoulder between the tip and a proximal portion consisting of a sclerotized shaft and a less refractile basal extension of the core. Tail usually attached posteroventrally, but sometimes terminally or posterodorsally, in a more or less distinct depression of the body. Entire body and tail covered with fine spines, often longer or more pronounced on ventral sucker and at tip of tail. Cuticle of body usually with minute papillae, each with a delicate filamentous process. Prepharynx short, pharynx present, esophagus and short ceca sometimes evident. Genital primordium dorsal and posterior to ventral sucker, basically C-shaped, but frequently with lobes representing the developing reproductive organs. Cephalic glands three pairs, more or less in a line on each side of the body, and numbered from anterior to posterior in subsequent descriptions; their ducts in a single bundle or with one duct median to others on each side of forebody. Excretory bladder U- to V-shaped or saccate, its epithelium more evident in some species than in others. Main excretory tubules divide at or posterior to level of ventral sucker to receive an anterior and a posterior collecting tubule, each with three groups of flame cells so that their formula is 2 $[(n + n + n) + (n + n + n)]$ with $n = 2$ or 3. Cystogenous glands not obvious, parenchyma usually with refractile spherules resembling oil droplets. Cercariae produced by small spherical to oval sporocysts in the digestive gland of the host and difficult to separate from that tissue.

DESCRIPTION OF SPECIES
(All measurements are in millimeters)

Cercaria tranoglandis Seitner, 1945
(Fig. 1)

Description (Based on larvae from one infected snail).—Body elongate-oval, 0.112-0.132 long, 0.056-0.069 wide, ends rounded in fixed specimens;

at least 9 papillae with setae on each side. Tail 0.081-0.097 long, 0.017-0.019 wide, its attachment postero-ventral; tip with enlarged spines. Oral sucker 0.038-0.049 long, 0.036-0.042 wide; virgula moderately large, 0.037-0.042 long, 0.034-0.038 wide, its right and left halves apparently not fused posteriorly. Stylet 0.020-0.022 long, 0.005 wide at base; tip curved ventrally, tapering gradually from shoulder, then abruptly toward point. Pharynx 0.006-0.010 long, 0.010-0.013 wide; esophagus and intestine not observed. Ventral sucker 0.019 in diameter, its anterior margin 0.073-0.075 from anterior end of body. Genital primordium C-shaped, with irregular margin. Cephalic glands lateral and anterior to ventral sucker with ducts in a single bundle; first pair with coarsest granules, granules of second and third pair finer and nearly equal in size; affinity for neutral red (*intra vitam*) greatest in third pair, less in first, and least in second. A pair of granular bodies at pharyngeal level stain intensely with neutral red. Excretory bladder U- to V-shaped; remainder of excretory system not observed. Sporocysts round to oval, to 0.200 in length.

Host.—Goniobasis livescens.

Locality and time of year.—Tippecanoe River, Indiana; August.

Cercaria tranoglandis is distinguished by the coarsely granular, refractile cytoplasm of the first pair of cephalic glands, the finer granules and similar texture of the second and third pair, and the affinity of the third pair for neutral red; the cephalic gland ducts in a single bundle; the granular bodies at the level of the pharynx; the postero-ventral attachment of the tail, and the long spines at its tip.

Emergence of this species was not observed precisely, but it seemed to occur at all hours. Periods of swimming towards the surface alternate with intervals during which the larvae rest and settle slowly in the water. Older ones may creep along the bottom of the container, inchworm fashion.

C. tranoglandis failed to penetrate dragonfly and damselfly naiads (*Ophiogomphus*? sp., *Calopteryx* sp.); mayfly naiads (*Stenonema*? sp.); and alderfly larvae (*Sialis* sp.).

Cercaria tremaglandis n. sp.
(Figs. 2-5)

Specific diagnosis (Based on infections in 4 snails).—Body elongate-oval, 0.118-0.135 long, 0.043-0.064 wide, ends often truncate on fixation; at least 7 papillae with setae on each side. Tail 0.066-0.096 long, 0.013-0.018 wide, attached posteroventrally; tip without enlarged spines. Oral sucker 0.040-0.058 long, 0.035-0.056 wide, with a pair of granular bodies staining deeply with neutral red immediately anterior to virgula organ. Virgula of moderate size, 0.035-0.047 long, 0.030-0.052 wide, its right and left halves not fused posteriorly. Stylet with a length of 0.014-0.019 divided as follows: tip 0.004-0.005, shoulder 0.002-0.003, shaft 0.006-0.008, base 0.0025-0.004; width at shoulder 0.0045-0.006, at base 0.005-0.007. Tip of stylet curved ventrally, tapering gradually from shoulder and then more abruptly toward point (Fig. 3); edges of shaft incurved. Pharynx 0.007-0.012 by 0.010-0.014; esophagus and intestine not observed. Ventral sucker 0.015-0.019 in diameter, with enlarged spines; its anterior margin 0.054-0.073 from anterior end of body. Genital primordium roughly C-shaped with an elongate posterior lobe. Cephalic glands

posterior and lateral to slightly anterior to ventral sucker with ducts in a single bundle; third pair with slightly coarser granules and a slight affinity for neutral red whereas the other pairs are similar in appearance and do not stain with that dye. Excretory bladder U- to V-shaped; main excretory tubules divide posterior to ventral sucker, at level of second or third cephalic gland; flame cell formula 2 [(2 + 2 + 2) + (2 + 2 + 2)]. Sporocyst subspherical, 0.125-0.145 in diameter, containing few embryos.

Host.—Pleurocera acuta.

Localities and time of year.—Wabash and Tippecanoe Rivers, Indiana; June to November.

Cercaria tremaglandis is distinguished by the two granular bodies anterior to the virgula organ, the relative similarity of the cephalic glands in texture and staining reaction, the single bundle of cephalic gland ducts, the abruptly tapering tip of the stylet, and the flame cell pattern.

The cercariae emerged mostly in the late evening and to some extent in the early evening but at no other times. On emergence, their swimming periods are rather prolonged with the larvae not moving in an up and down path as in some of the other species. Instead they swim upwards, usually stop short of the surface, and as they sink through the water, they slowly extend and contract the body and tail. The larvae may resume swimming on or before reaching the bottom of the container, or they may creep over the bottom, especially after they have been shed for some time. No phototactic response was observed.

Cercaria tremaglandis failed to enter dragonfly naiads (*Gomphus* spp., *Hagenius* sp.); caddis fly larvae (*Hydropsyche* sp.); and a small crayfish. It entered and encysted in a stonefly naiad (*Pteronarcys*? sp.) and occasionally mayfly naiads (*Hexagenia limbata*). Seventeen *Hexagenia* naiads from a stream in which virgulate cercariae evidently did not occur were exposed to infection. Of 11 examined 3 hours to 42 days later, five contained metacercariae, probably of *C. tremaglandis*. The longer the interval between exposure and examination, the fewer the metacercariae that were found. The six remaining naiads were held for 14-53 days after which one was fed to each of three newly hatched chicks and the remainder to two hamsters. Examination of these animals three to four days later yielded no trematodes.

Approximately 100 tailless cercariae and recently encysted metacercariae were found in the body cavity of one *Hexagenia* naiad three hours after exposure. The virgula organ and cephalic glands were largely depleted, but the species could be identified by their remnants and by the size and shape of the stylet. The newly formed cysts were spherical and 0.096-0.125 in diameter. Five from a naiad examined 42 days after exposure were spherical (about 0.135 in diameter) to oval (0.162 by 0.096), and had a thick double wall in which was embedded a stylet matching that of *C. tremaglandis*. The body was spiny, and the excretory bladder voluminous, U- to V-shaped, and filled with small concretions not over 0.008 in diameter.

Cercaria notura n. sp.
(Figs. 6-9)

Specific diagnosis (Based on infections in 3 snails).—Body elongate-oval, 0.101-0.158 long, 0.047-0.075 wide, ends usually slightly truncated on fixation; at least one papilla on each side. Tail attached dorsally near posterior end of body, length 0.064-0.097, width 0.013-0.020; with spines longer than on body and somewhat enlarged at tip of tail. Oral sucker 0.035-0.052 long, 0.028-0.051 wide; virgula small to moderate in size, 0.025-0.044 long, 0.027-0.050 wide, its right and left halves not fused posteriorly. Stylet length 0.018-0.019 divided as follows: tip 0.003-0.005, shoulder 0.0025-0.004, shaft 0.009-0.010, base 0.0015-0.0035; width at shoulder 0.0045-0.006, at base 0.004-0.005. Tip of stylet curved ventrally, edges of shaft straight or slightly incurved. Pharynx 0.006-0.008 long, 0.008-0.013 wide; esophagus and intestine not observed. Ventral sucker 0.016-0.022 in diameter; spines around its opening not noticeably enlarged; its anterior margin 0.060-0.087 from anterior end of body. Genital primordium variable, roughly C-shaped to irregularly or regularly lobed. Cephalic glands mostly lateral and posterior to ventral sucker, with ducts in a single bundle; first and third pairs with coarser granules than second pair, granules of first pair being largest. Affinity for neutral red greatest in third pair, less in first and least in second pair. Excretory bladder U- to V-shaped; main excretory tubules divide posterior to ventral sucker; flame cell formula 2 [(3 + 3 + 3) + (3 + 3 + 3)]. Sporocysts irregular, elongate-oval, or spherical, 0.086-0.264 long, 0.066-0.193 wide; usually with one or sometimes two protuberances and containing two to five developing cercariae.

Host.—Goniobasis livescens.

Localities and time of year.—Tippecanoe River, Indiana; June to August.

Cercaria notura is distinguished by the dorsal insertion of the tail, the coarse granules of the first cephalic gland and the intense affinity of the third for neutral red, the single bundle of cephalic gland ducts, and the 18 pairs of flame cells.

There was no apparent periodicity in emergence of the cercariae in the laboratory. They swim towards the surface in a distinctive, jerky, spinning manner and then rest as they settle to the bottom, slowly contracting and extending the body. This species is relatively inactive, and spends much of the time creeping or lying on the bottom, even when recently emerged. In this respect, it resembles *C. nothrica* Seitner but differs from that species in the length of the stylet, tail attachment, and host species. No reaction to light was observed.

Cercaria notura failed to enter various dragonfly and damselfly naiads (*Gomphus* sp., *Dromogomphus* sp., *Ophiogomphus*? sp., *Hetaerina americana, Ischnura*? sp., *Argia*? sp.); mayfly naiads (*Stenonema*? sp.); culicine mosquito larvae; and alderfly larvae (*Sialis* sp.).

Cercaria meringura Seitner, 1945
(Figs. 10-12)

Description (Based on infections in 3 snails).—Body relatively large, elongate-oval, 0.157-0.200 long, 0.076-0.114 wide, ends slightly truncate or rounded in heat killed specimens; at least 7 papillae with setae on each side.

Tail attached posteroventrally; 0.099-0.142 long, 0.023-0.030 wide; spinose with spines enlarged at its tip. Oral sucker 0.052-0.073 long, 0.041-0.055 wide; virgula organ conspicuous, 0.027-0.056 long, 0.027-0.053 wide, its right and left halves not fused posteriorly. Stylet length 0.044-0.049 divided as follows: tip 0.010-0.0105, shoulder 0.003-0.004, shaft 0.030-0.033, base 0.002-0.0035; width at shoulder 0.0055-0.007, at base 0.0065-0.008. Tip of stylet curved slightly ventrally, at first tapering gradually from shoulder and then more abruptly toward point; edges of shaft slightly incurved. Pharynx 0.011-0.014 long, 0.0155-0.018 wide; esophagus and intestine not observed. Ventral sucker 0.024-0.028 in diameter, its anterior margin 0.078-0.114 from anterior end of body, opening surrounded by enlarged spines. Genital primordium roughly C-shaped, with one or two rounded posterior lobes. Cephalic glands lateral to ventral sucker and tending to be more posterior than anterior to that sucker; their ducts in a single bundle; all 3 pairs with similar, coarse granules, the third pair only staining with neutral red. Pairs of small, granular bodies near ventral surface from level of pharynx to posterior edge of ventral sucker. Excretory bladder saccate and distinctly epithelial; main excretory tubules divide at level of ventral sucker; flame cell formula 2 [(3 + 3 + 3) + (3 + 3 + 3)]. Sporocyst up to 0.250 long, containing about 12 cercariae.

Host.—Goniobasis livescens.

Locality and time of year.—Tippecanoe River, Indiana; July to November.

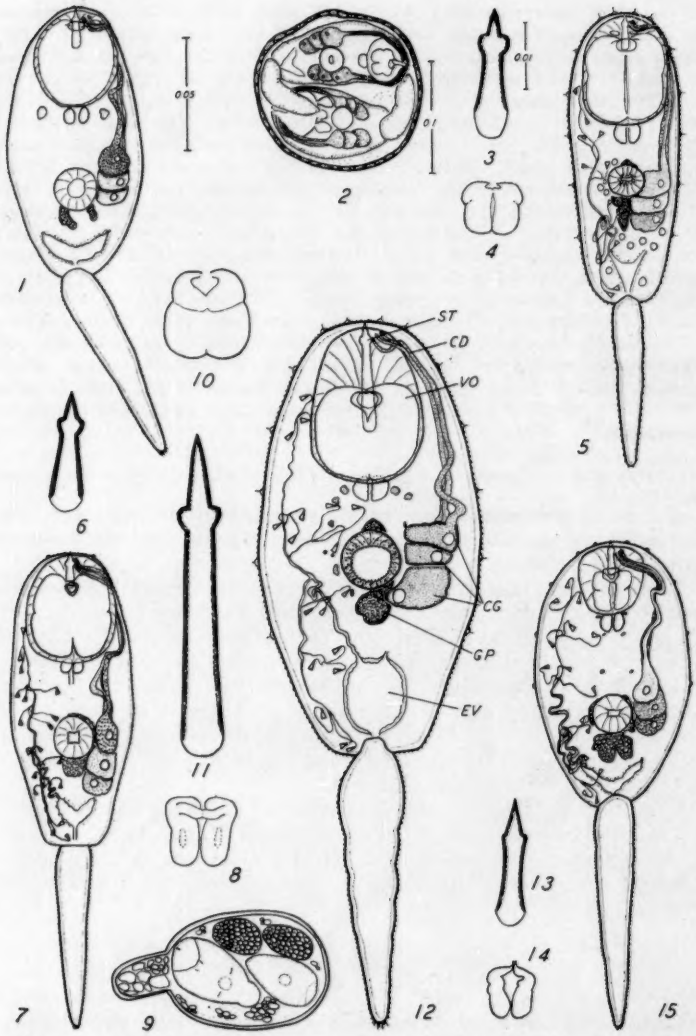
Cercaria meringura is readily distinguished by its large size, the long stylet, the saccate excretory bladder, and the uniformly coarse texture of the cephalic glands.

Some of the snails infected with *C. meringura* were collected in November and held in the laboratory until February for study. At that time, cercariae were shed only in the evening, usually after 9 o'clock. On emergence, they are strong swimmers and stay well above the bottom of the container, but are seldom found near the surface. Swimming periods of at least 1.5 minutes are followed by shorter rest periods during which the larvae sink towards the bottom. As in other species, the older cercariae seldom leave the bottom of the container. No phototactic response was observed.

C. meringura failed to enter dragonfly and damselfly naiads (*Gomphus* sp., *Stylurus spiniceps, Dromogomphus* sp., *Hagenius* sp., *Boyeria* sp., *Macromia* sp., *Calopteryx*? sp., *Ischnura*? sp., *Argia*? sp.); mayfly naiads (*Stenonema*? sp.); alderfly larvae (*Sialis* sp.); and beetle larvae (*Psephenus* sp.).

Cercaria papiliogona n. sp.
(Figs. 13-15)

Specific diagnosis (Based on infections in 7 snails).—Body small, broadly oval, 0.088-0.127 long, 0.053-0.075 wide, ends usually rounded in fixed specimens, rarely truncate; at least 5 papillae on each side. Tail attached posteroventrally, 0.084-0.119 long, 0.013-0.018 wide, with spines longer than on body, somewhat enlarged at tip of tail. Oral sucker 0.027-0.033 long, 0.024-0.032 wide, virgula small, 0.013-0.025 long, 0.015-0.023 wide, its right and left halves not fused posteriorly. Stylet length 0.017-0.021, divided as follows: tip



Figs. 1-15.—All figures except those of virgula organs in living specimens are free hand to scale from numerous measurements of specimens killed in hot 3 percent formalin. Figures of entire cercariae are drawn to the same scale; stylets are represented at 3.0 times, sporocysts and metacercariae at 0.5 times that magnification. 1. *Cercaria tranoglandis*, fully developed specimen, ventral view. 2-5. *Cercaria tremaglandis*. 2. Living sporocyst. 3. Stylet, ventral view.

0.0045-0.006, shoulder 0.002-0.0035, shaft 0.007-0.009, base 0.002-0.003; width at shoulder 0.004-0.005, at base 0.004-0.006. Tip of stylet curved ventrally but straight in dorsal view, shoulder region often indistinct, edges of shaft incurved. Pharynx 0.006-0.012 long, 0.009-0.012 wide; esophagus and intestine not observed. Ventral sucker 0.016-0.019 in diameter, its anterior margin 0.055-0.070 from anterior end of body, spines around opening slightly enlarged. Genital primordium consistently tetralobate, butterfly-shaped. Cephalic glands lateral to ventral sucker and tending to be more anterior than posterior to that sucker; their ducts in a single bundle; third pair with coarsest granules and greatest affinity for neutral red, granules of second pair larger than those of first. Small, paired, granular structures staining with neutral red situated on either side of the pharynx and posterior to that level. Excretory bladder U- to V-shaped; main excretory tubules divide lateral or posterior to ventral sucker; flame cell formula 2 [(3 + 3 + 3) + (3 + 3 + 3)]. Sporocysts not studied.

Host.—Pleurocera acuta.

Localities and time of year.—Wabash and Tippecanoe Rivers, Indiana; May to August.

Cercaria papiliogona is distinguished by the shape of the genital primordium and virgula organ which is not fused posteriorly, the coarse texture and deep staining reaction of the third pair of cephalic glands, the indistinct shoulders of the stylet, the flame cell formula, and the shape of the body on fixation.

This species emerged at all hours but in larger numbers during the evening. At first, the swimming movement is prolonged with the cercariae remaining near the bottom, rising and falling slowly and with steady progression. The larvae rest body downward at the bottom of the container with little contracting and extending of the body. As the cercariae age, swimming movements are less prolonged and consist of a jerky, upward spinning; eventually most of the time is spent resting or creeping along the bottom. At room temperature, the cercariae live for 22-40 hours after emergence. There was some evidence of a slight positive response to light.

C. papiliogona failed to enter dragonfly and damselfly naiads (*Gomphus* sp., *Stylurus spiniceps, Dromogomphus* sp., *Ophiogomphus*? sp., *Macromia* sp., *Calopteryx* sp., *Hetaerina americana, Ischnura*? sp., *Argia*? sp.); mayfly naiads (*Hexagenia limbata, Stenonema*? sp.); caddis fly larvae (*Cheumatopsyche*? sp., *Hydropsyche* sp., and

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4. Outline of virgula organ in living specimen, ventral view. 5. Fully developed cercaria, ventral view. 6-9. *Cercaria notura.* 6. Stylet, ventral view. 7. Fully developed cercaria, ventral view. 8. Outline of virgula organ in living specimen, ventral view. 9. Living sporocyst. 10-12. *Cercaria meringura.* 10. Outline of virgula organ in living specimen, ventral view. 11. Stylet, ventral view. 12. Fully developed cercaria, ventral view. 13-15. *Cercaria papiliogona.* 13. Stylet, ventral view. 14. Outline of virgula organ in living specimen, ventral view. 15. Fully developed cercaria, ventral view.

Abbreviations: CD — Cephalic Gland Duct; CG — Cephalic Gland; EV — Excretory Vesicle; GP — Genital Primordium; ST — Stylet; VO — Virgula Organ.

one unidentified species); stonefly naiads (*Perlinella* sp., and one unidentified species); culicine mosquito larvae; chironomid larvae; alderfly larvae (*Sialis* sp.); two unidentified species of beetle larvae; and crayfish.

Cercaria pinguisoma n. sp.
(Figs. 16-19)

Specific diagnosis (Based on infections in 2 snails).—Body broadly oval, 0.114-0.144 long, 0.061-0.078 wide; anterior end usually rounded, posterior end truncate on fixation; cuticular papillae not observed but may be present. Tail attached posteroventrally; length 0.089-0.119, width 0.015-0.020; spines larger than on body, but not pronounced at its tip. Oral sucker 0.046-0.063 long, 0.043-0.053 wide; virgula moderately large, 0.030-0.048 long, 0.036-0.045 wide, its right and left halves not fused posteriorly. Stylet length 0.027-0.029 divided as follows: tip 0.007-0.008, shoulder 0.004-0.0045, shaft 0.011-0.0125, base 0.005-0.006; width at shoulder 0.006-0.0065, at base 0.0075-0.008. Tip of stylet curved ventrally, tapering gradually from shoulder, then more abruptly toward point. Pharynx 0.0075-0.010 long, 0.010-0.013 wide; esophagus and ceca short, the latter not reaching ventral sucker. Ventral sucker 0.017-0.021 in diameter, its anterior margin 0.066-0.073 from anterior end of body; spines around its opening not enlarged. Genital primordium roughly C-shaped with 2 rounded posterior lobes. Cephalic glands lateral to ventral sucker and tending to be more anterior than posterior to that sucker, with ducts in a single convoluted bundle; first pair with the largest granules; granules of third pair larger than those of second pair; all glands except second pair with a pronounced affinity for neutral red. Small, paired granular structures staining with that dye on either side of pharynx, esophagus, and ventral sucker. Excretory bladder U- to V-shaped; main excretory tubules divide at level of posterior border of ventral sucker; flame cell formula 2 [(3 + 3 + 3) + (3 + 3 + 3)]. Sporocyst subspherical to ovoid, 0.135-0.193 long, 0.107-0.128 wide; containing up to 8 developing cercariae.

Host.—Goniobasis livescens.

Locality and time of year.—Tippecanoe River, Indiana; July to September.

Cercaria pinguisoma is characterized by the broadly oval body shape, relatively large stylet, the moderately large, unfused virgula organ, the texture and staining reaction of the cephalic glands and the arrangement of their ducts, the paired granular masses in the forebody, attachment of the tail, and the flame cell pattern.

This species is usually shed during the early evening hours. On emergence, the cercariae are very active and swim continuously well above the bottom of the container with very occasional rest periods. Progressive inchworm movements are common after the first hour; some hours later the cercariae are found lying motionless on their backs on the bottom of the dish. This species showed a marked tendency to encyst on the slide when mounted for study. Phototropic reactions were not observed.

C. pinguisoma failed to enter dragonfly and damselfly naiads (*Gomphus* sp., *Calopteryx* sp., *Hetaerina americana*); mayfly naiads (*Stenonema*? sp.); beetle larvae (*Psephenus* sp.); and crayfish.

Cercaria bryobulga n. sp.
(Figs. 20-22)

Specific diagnosis (Based on infections in 3 snails).—Body relatively large, elongate-oval, 0.169-0.193 long, 0.056-0.068 wide; usually the anterior end rounded and posterior end truncate on fixation; cuticular papillae not observed but may be present. Tail attached posteroventrally; length 0.079-0.117, width 0.015-0.018; its tip without enlarged spines. Oral sucker 0.058-0.068 long, 0.049-0.062 wide; virgula organ extremely large, 0.054-0.059 long, 0.048-0.058 wide, its right and left halves not fused posteriorly. Stylet length 0.021-0.024, divided as follows: tip 0.005, shoulder 0.003, shaft 0.010, base 0.0045; width at shoulder 0.006, at base 0.007-0.008. Tip of stylet curved ventrally, edges of shaft straight. Pharynx 0.008-0.011 long, 0.013-0.015 wide; esophagus and intestine not observed. Ventral sucker 0.017-0.022 in diameter, its anterior margin 0.086-0.092 from anterior end of body; with enlarged spines around its opening. Genital primordium C-shaped, largely dorsal to ventral sucker. Cephalic glands anterior, lateral, and posterior to ventral sucker, with ducts in a single bundle; third pair with coarse granules, first and second pair similar, with fine granules. Two pairs of small granular bodies staining with neutral red on each side of body immediately anterior to ventral sucker. Excretory bladder small, saccate, distinctly epithelial; main excretory tubules divide lateral to posterior border of ventral sucker; flame cell pattern not determined. Sporocysts not observed.

Host.—Goniobasis sp.

Locality and time of year.—Pere Marquette River, Michigan; September.

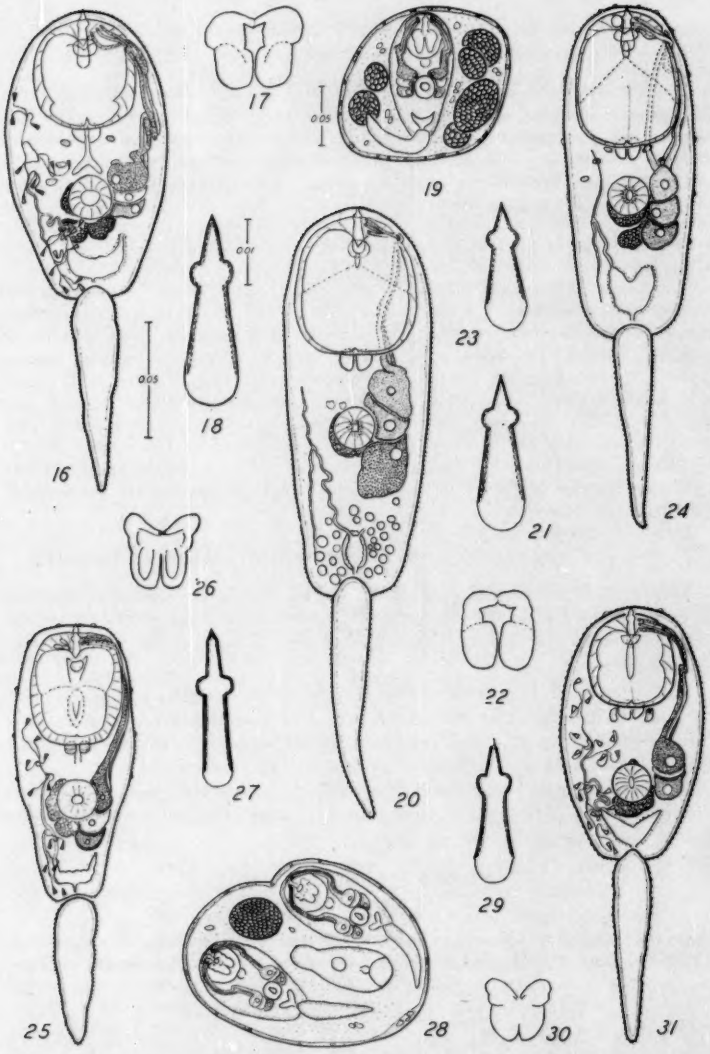
Cercaria bryobulga is characterized by the large, unfused virgula, the size of the body, the texture of the cephalic glands, the granular structures near the ventral sucker, and the shape of the small excretory bladder.

Emergence of this species was not followed closely, but seemed to occur at all hours. The cercariae are strong swimmers and stay well above the bottom of the container. Creeping movements were not observed, nor was any definite reaction to light noted.

C. bryobulga did not enter dragonfly and damselfly naiads (*Dromogomphus* sp., *Hetaerina americana*); and stonefly naiads (two unidentified species).

Cercaria neusticoides n. sp.
(Figs. 23-24)

Specific diagnosis (Based on infection in one snail).—Body elongate-oval, 0.132-0.150 long, 0.050-0.061 wide, ends rounded to slightly truncate on fixation, at least 7 papillae on each side. Tail attached posteroventrally, length 0.083-0.090, width 0.015-0.017; tip without enlarged spines. Oral sucker 0.059-0.063 long, 0.044-0.050 wide, with a pair of refractile spherules, one on each side of stylet at level of shoulder. Virgula large, 0.049-0.055 long, 0.041-0.049 wide, its right and left halves not fused posteriorly. Stylet length 0.018-0.022, divided as follows: tip 0.0035-0.005, shoulder 0.003, shaft 0.008, base 0.004; width at shoulder 0.004-0.005, at base 0.005-0.007. Tip of stylet curved ventrally; edges of shaft nearly straight. Pharynx 0.007-0.009 long, 0.011-0.013 wide; esophagus and intestine not observed. Ventral sucker 0.017-0.020 in diameter, its anterior margin 0.071-0.078 from anterior end of body;



Figs. 16-31.—16-19. *Cercaria pinguisoma.* 16. Fully developed cercaria, ventral view. 17. Outline of virgula organ in living specimen, ventral view. 18. Stylet, ventral view. 19. Living sporocyst. 20-22. *Cercaria bryobulga.* 20. Fully developed cercaria, ventral view. 21. Stylet, ventral view. 22. Outline of virgula organ in living specimen, ventral view. 23-24. *Cercaria neusticoides.* 23. Stylet, ventral view. 24. Fully developed cercaria, ventral view. 25-27.

with enlarged spines around opening. Genital primordium roughly C-shaped. Cephalic glands lateral to ventral sucker and tending to be more posterior than anterior to that sucker; with one duct on each side median to the other 2 in a bundle; texture of all glands nearly equal, the third pair with slightly the coarsest granules and greatest affinity for neutral red. Small, paired, granular structures staining with that dye on either side of body from pharynx to ventral sucker. Excretory bladder U- to V-shaped; main excretory tubules divide just posterior to level of ventral sucker; flame cell pattern not determined. Sporocysts not studied.

Host.—Pleurocera acuta.

Locality and time of year.—Tippecanoe River, Indiana; May.

Cercaria neusticoides resembles closely the cercaria of *Mosesia chordeilesia* (syn. *Cercaria neustica* Seitner) in texture and staining reaction of the cephalic glands and in the arrangement of their ducts. It is distinguished from that species by the large, unfused virgula organ, the presence of paired granular structures in the forebody, and the refractile spherules on either side of the stylet.

The time of emergence varies, but there is a tendency for the snail to shed more cercariae in the late afternoon and evening than at other hours. Swimming movements are similar to those of other virgulate species. There seemed to be a slight preference for light areas of the container, but no marked phototropic reaction was observed. The cercariae lived for 22 to 41 hours after emergence.

Cercaria neusticoides failed to enter dragonfly and damselfly naiads (*Gomphus* spp., *Dromogomphus* sp., *Ischnura*? sp., *Argia*? sp.); but penetrated one species of mayfly naiad (*Stenonema*? sp.) without encysting and repeatedly entered and encysted in the body cavity of another species (*Hexagenia limbata*). Actual penetration was not observed, but the cercariae could be seen attaching to various parts of the naiad. The primary cyst is formed within three hours of penetration, measures 0.091-0.121 in diameter, and yields to the movements of the worm; the virgula organ shows varying degrees of depletion but is usually distinct.

Twenty naiads of *Hexagenia limbata* were exposed to *C. neusticoides*. Difficulties were encountered in keeping the insects alive in the laboratory, but there was evidence that the metacercariae did not survive for more than a few days. Thus, *Hexagenia limbata* may not be the natural second intermediate host of *C. neusticoides*.

Cercaria pyxiceps n. sp.
(Figs. 25-27)

Specific diagnosis (Based on an infection in one snail).—Body 0.106-0.120 long, 0.050-0.059 wide, shape characteristic on fixation (Fig. 25) with ends

Cercaria pyxiceps. 25. Fully developed cercaria, ventral view. 26. Outline of virgula organ in living specimen, ventral view. 27. Stylet, ventral view. 28-31. *Cercaria celatoglandis.* 28. Living sporocyst. 29. Stylet, ventral view. 30. Outline of virgula organ in living specimen, ventral view. 31. Fully developed cercaria, ventral view.

almost always truncate; at least 5 papillae on each side. Tail attached terminally and easily lost, 0.063-0.073 long, 0.014-0.018 wide; with spines larger than on body but not pronounced at tip. Oral sucker 0.045-0.048 long, 0.036-0.044 wide, with 2 pairs of granular bodies staining deeply with neutral red immediately anterior to virgula organ. Virgula of moderate size, 0.033-0.043 long, 0.033-0.038 wide, its right and left halves not fused posteriorly. Stylet length 0.0215-0.023, divided as follows: tip 0.007-0.0075, shoulder 0.002-0.004, shaft 0.008-0.011, base 0.0015-0.0025; width at shoulder 0.0055-0.007, at base 0.004-0.005. Tip of stylet curved ventrally, tapering gradually from shoulder and then more abruptly toward point; edges of shaft almost straight. Pharynx 0.006-0.008 long, 0.011-0.013 wide; posterior part of esophagus and intestine not observed. Ventral sucker 0.017-0.018 in diameter, anterior margin 0.063-0.070 from anterior end of body; without conspicuous spines around opening. Genital primordium roughly C-shaped with rounded posterior lobes. Cephalic glands lateral and posterior to ventral sucker, with ducts in a single bundle; first pair with the coarsest granules, third pair refractile and with coarser granules than second pair; third pair with the greatest affinity for neutral red. Excretory bladder U-shaped; main excretory tubules divide at level of second pair of cephalic glands; flame cell formula 2 [(2 + 2 + 2) + (2 + 2 + 2)]. Sporocysts not studied.

Host.—Pleurocera acuta.

Locality and time of year.—Tippecanoe River, Indiana; June.

Cercaria pyxiceps is characterized by the shape of the body after fixation, the paired granular structures in the oral sucker, the terminal attachment of the tail, the shape of the stylet, and the flame cell formula.

The cercariae usually emerge in the evening and at first swim freely for prolonged periods between which they pause to rest, floating at or near the surface. Later much of the time is spent creeping on the bottom of the container or resting with flexing rather than contracting and extending movements of the body. No distinct reaction to light was observed. *C. pyxiceps* showed a marked tendency to discharge the contents of the first pair of cephalic glands and form a cyst on the slide when living specimens were mounted for study.

Cercaria celatoglandis n. sp.
(Figs. 28-31)

Specific diagnosis (Based on an infection in one snail).—Body broadly oval, 0.103-0.124 long, 0.053-0.064 wide; anterior end usually rounded, posterior end truncate on fixation; at least one papilla on each side. Tail attached posteroventrally, length 0.059-0.085, width 0.015-0.018; tip without enlarged spines. Oral sucker 0.037-0.042 long, 0.034-0.038 wide; virgula small to moderate, 0.030-0.033 long, 0.030-0.036 wide, its right and left halves not fused posteriorly. Stylet length 0.018-0.021, divided as follows: tip 0.004-0.0045, shoulder 0.003-0.0035, shaft 0.0085-0.0095, base 0.0015-0.0045; width at shoulder 0.005-0.0055, at base 0.0055-0.006. Tip of stylet curved ventrally, tapering gradually from shoulder and then more abruptly toward point; edges of shaft incurved. Pharynx 0.0075-0.008 long, 0.0105-0.0125 wide; esophagus and intestine not observed. Ventral sucker 0.0175-0.018 in diameter, its anterior margin 0.064-0.071 from anterior end of body; without enlarged

spines around opening. Genital primordium roughly C-shaped. Cephalic glands anterior and lateral to ventral sucker with ducts in a single bundle; first and third pairs with coarse granules, the latter with the greatest affinity for neutral red; second pair inconspicuous, with fine granules and no affinity for neutral red, often concealed by first pair. A small granular body staining with neutral red on either side of pharynx. Excretory bladder U- to V-shaped, main excretory tubules divide laterally to ventral sucker; flame cell formula 2 [(3 + 3 + 3) + (3 + 3 + 3)]. Sporocysts rounded, oval or irregular; 0.150-0.288 long, 0.121-0.164 wide; containing up to 5 developing cercariae.

Host.—Goniobasis livescens.

Locality and time of year.—Tippecanoe River, Indiana; July.

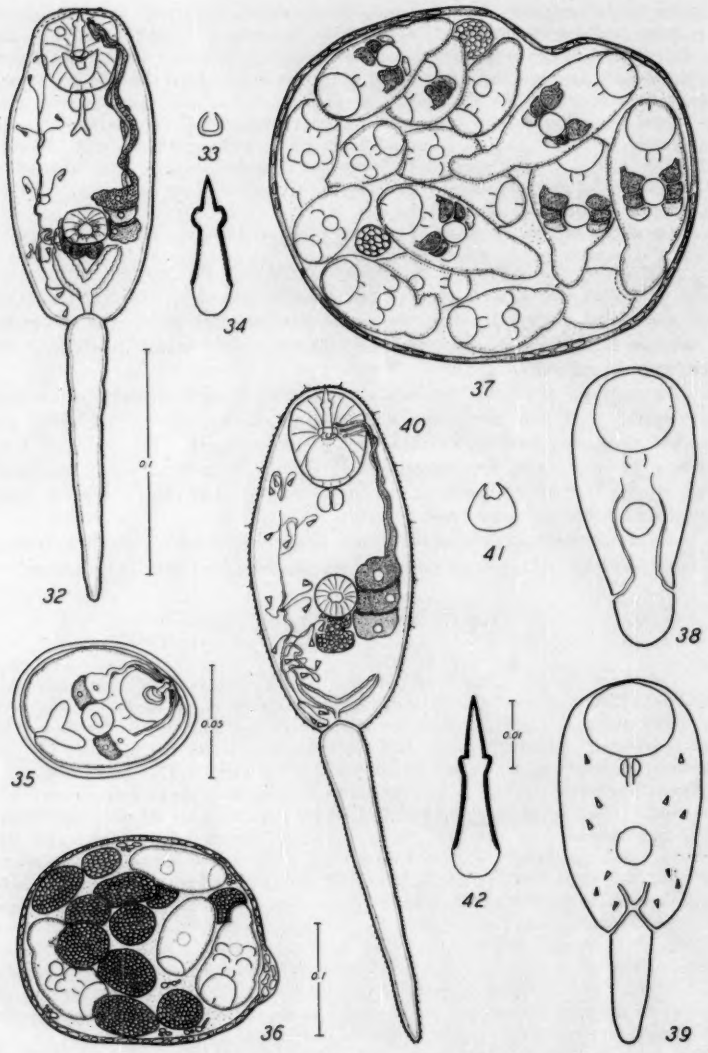
Cercaria celatoglandis is characterized by the coarse texture of the first and third pairs of cephalic glands, the deep staining reaction of the third pair, and the inconspicuous second pair; the granular body on either side of the pharynx; the relatively small stylet; and the excretory pattern.

Emergence is chiefly nocturnal and swimming is at first prolonged. Creeping, and extending and contracting movements of the body are common during rest periods and in older cercariae. There was a tendency towards cyst formation when living specimens were mounted for study, but no encystment occurred in the containers. Phototropic reactions were not observed.

C. celatoglandis did not enter dragonfly and damselfly naiads (*Gomphus* sp., *Hetaerina* sp.) and an unidentified caddis fly larva.

Cercaria adoxovirgula n. sp.
(Figs. 32-36)

Specific diagnosis (Based on infections in 5 snails).—Body elongate-oval; 0.096-0.145 long, 0.048-0.086 wide; ends rounded to truncate, cuticle consistently pulling away from body on fixation; at least one papilla on each side. Tail attached posteroventrally, 0.102-0.146 long, 0.013-0.020 wide; its tip without enlarged spines. Oral sucker 0.026-0.039 long, 0.027-0.037 wide, with refractile spherule on each side of stylet at level of shoulder. Virgula extremely small; 0.008-0.020 long, 0.011-0.024 wide; appearing as an obscure, refractile ring surrounding the oral cavity in living specimens; its right and left halves fused posteriorly. Stylet 0.019-0.022 long, tip 0.0045-0.006, shoulder 0.002-0.004, shaft 0.0075-0.0095, base 0.0035-0.0055; width at shoulder 0.004-0.006, at base 0.0045-0.007. Tip of stylet curved ventrally, its lateral edges curving toward point; edges of shaft straight or slightly incurved. Pharynx 0.007-0.010 long, 0.009-0.0115 wide; esophagus and ceca short, the latter terminating about 1/3 of the body length from anterior end. Ventral sucker 0.018-0.022 in diameter, its anterior margin 0.052-0.091 from anterior end of body; its opening surrounded by enlarged spines. Genital primordium roughly C-shaped to tetralobate. Cephalic glands lateral and anterior to ventral sucker, with ducts in a single bundle; first pair with the largest granules, granules of third pair larger than those of second; third pair with the greatest affinity for neutral red, first pair staining more than second pair. Excretory bladder U- to V-shaped, its epithelial nature evident; main excretory tubules divide lateral or posterior to ventral sucker; flame cell formula 2 [(2 + 2 + 2) +



Figs. 32-42.—32-36. *Cercaria adoxovirgula.* 32. Fully developed cercaria, ventral view. 33. Outline of virgula organ in living specimen, ventral view. 34. Stylet, ventral view. 35. Living metacercaria from body cavity of caddis fly larva 8 hours after exposure to cercariae. 36. Living sporocyst. 37-42. *Cercaria cordivirgula.* 37. Living sporocyst. 38. Developing cercaria showing open-

(2 + 2 + 2)]. Sporocysts round to oval, 0.218 long, 0.185 wide, containing up to 15 developing cercariae.

Host.—Pleurocera acuta.

Localities and time of year.—Wabash and Tippecanoe Rivers, Indiana; August and September.

Cercaria adoxovirgula is distinguished by the small, fused, virgula organ; the coarse granules of the first pair of cephalic glands, and the intense affinity of the third pair for neutral red; the pair of refractile spherules in the oral sucker; and the flame cell pattern.

Emergence of this species is almost entirely at night. Natatory movements are similar to those of other virgulate species except that the body is usually more extended and swimming periods are considerably shorter, usually no longer than 30 seconds, and always less than three minutes. The cercariae usually swim upwards, stopping at or near the surface. Several hours after emergence, they rarely leave the bottom of the container where they lie motionless or slowly contract and extend the body. There was some tendency to form a cyst when mounted for study, but no encystment occurred in the containers. There were no definite reactions to light.

C. adoxovirgula failed to penetrate various dragonfly and damselfly naiads (*Gomphus* sp., *Dromogomphus* sp., *Ophiogomphus*? sp., *Calopteryx* sp., *Hetaerina americana, Ischnura*? sp.); mayfly naiads (*Hexagenia limbata, Stenonema*? sp.); stonefly naiads (*Perlinella*? sp. and one unidentified species); and crayfish. Large numbers entered but did not encyst in an alderfly larva (*Sialis* sp.) on one occasion, but later attempts to repeat the experiment were unsuccessful. On several occasions, penetration and encystment were observed in various chironomid larvae, but work with those insects was hindered by difficulties in keeping them alive in the laboratory.

Penetration and encystment also occurred repeatedly on exposure of caddis fly larvae (*Hydropsyche* sp.) from a stream in which virgulate cercariae were not found. Formation of the cyst occurs within seven hours after penetration (Fig. 35). It is oval, 0.073-0.092 long, 0.053-0.068 wide; the primary cyst wall is thin and hyaline with a pinkish cast. The first pair of cephalic glands is depleted, and the virgula organ has lost some of its contents but is still recognizable.

Fifty hydropsychid larvae were exposed to *C. adoxovirgula* and placed in aerated water in battery jars with stones and gravel from the natural habitat of the larvae, but they could not be kept alive longer than four to six weeks. Examination of dead or dying larvae indicated that the metacercariae did not survive longer than three days. It thus seems that the hydropsychid species used is not the natural second intermediate host of *C. adoxovirgula.*

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ings of primary excretory tubules. 39. Later stages of developing cercaria showing fusion of primary excretory tubules. 40. Fully developed cercaria, ventral view. 41. Outline of virgula organ in living specimen, ventral view. 42. Stylet, ventral view.

Cercaria cordivirgula n. sp.
(Figs. 37-42)

Specific diagnosis (Based on infections in 2 snails).—Body elongate-oval, 0.147-0.162 long, 0.066-0.079 wide, ends usually rounded on fixation; at least 6 papillae with setae on each side. Tail attached posteroventrally, 0.139-0.157 long, 0.018-0.0215 wide; its tip without enlarged spines. Oral sucker 0.041-0.044 long, 0.033-0.035 wide; virgula small, cordiform, 0.021-0.023 long, 0.022-0.025 wide, its right and left halves fused posteriorly in emerged cercariae. Stylet length 0.025-0.027, divided as follows: tip 0.008-0.009, shoulder 0.002-0.0035, shaft 0.010-0.012, base 0.0035-0.0045; width at shoulder 0.0045-0.0055, at base 0.006-0.0075. Edges of stylet shaft incurved. Pharynx 0.010-0.011 long, 0.011-0.012 wide; esophagus and intestine not observed. Ventral sucker 0.019-0.020 in diameter, anterior margin 0.078-0.086 from anterior end of body; without enlarged spines around opening. Genital primordium roughly C-shaped. Cephalic glands anterior, lateral, and posterior to ventral sucker, with ducts in a single bundle; first and second pairs with coarse granules and little or no affinity for neutral red; third pair refractile, finely granular, and staining with that dye. Excretory bladder U- to crescent-shaped, its epithelium pronounced; main excretory tubules divide posterior to ventral sucker; flame cell formula 2 [(3 + 3 + 3) + (3 + 3 + 3)]. Sporocysts round, oval, or irregular, 0.207-0.434 long, 0.171-0.356 wide, containing 6-21 developing cercariae.

Host.—Pleurocera acuta.

Locality and time of year.—Wabash River, Indiana; November.

Cercaria cordivirgula is distinguished by the small, fused, heart-shaped virgula organ, the shape of the stylet, the texture and staining reaction of the cephalic glands, and the flame cell pattern.

A few observations were made on developing cercariae, in some of which were seen the pair of mucoid-containing sacs which eventually fuse in the oral sucker to give rise to the virgula organ of the completely developed larva. In the youngest embryos in which features of the excretory system were observed (Fig. 38), the primary excretory pores were seen at the body-tail furrow and the primary tubules had not united. In more advanced embryos (Fig. 39), the tubules had fused to form the bladder and six flame cells were seen on each side of the body. Their capillaries and the primordium of the excretory epithelium were not observed.

Cercaria cordivirgula emerges mostly at night. Definite reactions to light were not evident. This species did not enter dragonfly and damselfly naiads (*Gomphus* sp., *Calopteryx* sp.); mayfly naiads (*Hexagenia limbata, Isonychia*? sp.); and caddis fly larvae (*Hydropsyche* sp.). Penetration of a stonefly naiad, *Isoperla* sp., by a limited number of cercariae was observed; encystment did not occur within 20 hours, however, and the experiment was not repeated.

DISCUSSION

In addition to the ten new species of virgulate cercariae described above, nine others have been reported from the United States. They

include the five species described by Seitner (1945), *Cercaria geddesi* Ameel 1939, the cercaria of *Cephalophallus obscurus* Macy and Moore 1954, and the cercariae of *Allassogonoporus vespertilionis* and *Acanthatrium oregonense* reported by Knight and Pratt (1955). Faust (1921) described two species of xiphidiocercariae from *Goniobasis carinifera* in Georgia. According to his description and figures, they may well be of the virgulate type and, for that reason, are included in the key below. One species, *Cercaria camilla,* is described as having "an enormous prepharyngeal pocket . . . with a thick semi-muscular, semi-mucoid wall." In the other, *Cercaria tabitha,* "the large oral sucker . . . is provided internally with a thick mucoid substance resembling that of the stylet."

KEY TO VIRGULATE XIPHIDIOCERCARIAE OF NORTH AMERICA
(All measurements of the virgula organ taken from specimens killed in hot 3 percent formalin)

1. With 2 pairs of cephalic glands. Stylet 0.014 long. ..... Cercaria of *Acanthatrium oregonense.*
   With 3 pairs of cephalic glands. 4
   With 4 pairs of cephalic glands. 2
2. Ducts of cephalic glands pass anteriorly in a single bundle. 3
   Ducts of one pair of cephalic glands median to those of others. ..... *Cercaria geddesi.*
3. Stylet blunt, with distinct shoulder region; sporocysts in *Goniobasis carinifera.* ..... *Cercaria tabitha.*
   Stylet sharp, without distinct shoulder, 0.024-0.027 long; sporocysts in *Fluminicola virens.* ..... Cercaria of *Cephalophallus obscurus.*
4. Virgula organ within oral sucker. 5
   Large virgula organ posterior (?) to oral sucker; sporocysts in *Goniobasis carinifera.* ..... *Cercaria camilla.*
5. Excretory bladder saccate, its epithelium distinct. 6
   Excretory bladder U-, V-, Y-, or crescent-shaped, its epithelial lining usually not distinct. 8
6. Stylet 0.044-0.049 long. ..... *Cercaria meringura.*
   Stylet not over 0.025. 7
7. Stylet 0.016 long; sporocysts in *Fluminicola virens.* ..... Cercaria of *Allassogonoporus vespertilionis.*
   Stylet 0.020-0.024 long, third pair of cephalic glands with coarser granules than others; sporocysts in *Goniobasis* sp. ..... *Cercaria bryobulga.*
8. Cephalic gland ducts extend anteriad in a single bundle. 10
   One pair of cephalic gland ducts median to others. 9
9. Virgula organ small, 0.019-0.027 long, fused posteriorly; no paired granular structures staining with neutral red near pharynx and ventral sucker. ..... Cercaria of *Mosesia chordeilesia.*
   Virgula organ large, 0.049-0.055, not fused posteriorly; granular structures present. ..... *Cercaria neusticoides.*
10. Stylet shorter than 0.024. 12
    Stylet longer than 0.024. 11
11. Stylet 0.025-0.027 long. Virgula organ small, 0.020-0.023 long, fused posteriorly. ..... *Cercaria cordivirgula.*

Stylet 0.027-0.029 long. Virgula organ 0.030-0.048 long, not fused posteriorly. ..... *Cercaria pinguisoma.*

12. Oral sucker with paired granular structures staining with neutral red anterior to virgula organ. 13
Oral sucker without such structures. 14
13. Two pairs of granular structures anterior to virgula organ. Stylet tip at least 0.007 long. Granules of first pair of cephalic glands decidedly coarser than in second pair. ..... *Cercaria pyxiceps.*
One pair of granular structures anterior to virgula organ. Stylet tip never longer than 0.005. Texture of first and second pairs of cephalic glands equal. ..... *Cercaria tremaglandis.*
14. First 2 pairs of cephalic glands of equal or nearly equal texture, granules of third pair distinctly coarser than others. ..... *Cercaria nyxetica.*
First 2 pairs of cephalic glands not similar in texture. 15
15. Second and third pairs of cephalic glands of equal or nearly equal texture. 16
Second and third pairs of cephalic glands of very different texture. 17
16. Anterior pair of cephalic glands exceedingly prominent, with very coarse granules. A pair of granular bodies at level of pharynx staining well with neutral red. ..... *Cercaria tranoglandis.*
Anterior pair of cephalic glands not prominent. No granular bodies near pharynx. ..... *Cercaria nothrica.*
17. Tail attachment posterodorsal. ..... *Cercaria notura.*
Tail attachment posteroventral. 18
18. Virgula organ fused posteriorly, indistinct, 0.008-0.020 long. Flame cell formula 2 [(2 + 2 + 2) + (2 + 2 + 2)]. ..... *Cercaria adoxovirgula.*
Virgula organ distinct, not fused posteriorly; flame cell formula 2 [(3 + 3 + 3) + (3 + 3 + 3)]. 19
19. Genital primordium C-shaped. Virgula organ 0.030-0.033 long; granules of first and third pairs of cephalic glands coarse, those of second pair very fine. ..... *Cercaria celatoglandis.*
Genital primordium tetralobate. Virgula organ 0.013-0.025 long; third pair of cephalic glands with coarsest granules, those of second pair coarser than in first pair. ..... *Cercaria papiliogona.*

SUMMARY

Twelve virgulate xiphidiocercariae are reported, ten as new species. They are *Cercaria tremaglandis* n. sp., *C. papiliogona* n. sp., *C. adoxovirgula* n. sp., *C. neusticoides* n. sp., *C. pyxiceps* n. sp., and *C. cordivirgula* n. sp., all from *Pleurocera acuta; Cercaria bryobulga* n. sp. from *Goniobasis* sp.; and *Cercaria notura* n. sp., *C. pinguisoma* n. sp., and *C. celatoglandis* n. sp. from *Goniobasis livescens.* The remaining two are *C. tranoglandis* Seitner and *C. meringura* Seitner which are redescribed.

The excretory pattern was determined for nine species and found to be either 2 [(2 + 2 + 2) + (2 + 2 + 2)] or 2 [(3 + 3 + 3) + (3 + 3 + 3)]. Observations on potential second intermediate hosts are recorded, and a key to the virgulate xiphidiocercariae of North America is included.

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Notes and Discussion

Additions to the Flora of Kalamazoo County, Michigan[1]

Since the establishment of Michigan State University's Kellogg Gull Lake Biological Station in 1954, Hanes' (*Flora of Kalamazoo County, Michigan: Vascular Plants,* The Anthoensen Press, Portland, Maine, 295 pp., 1947) Flora has become the basic reference for both the presence of species in the county and geographical location for unusual plants to be used in class demonstration. During the years that the Biological Station has been in operation, seventeen species not listed by the Hanes have been collected in the county.

Seven of these additional species are ruderal elements (see Dansereau, *Biogeography: An Ecological Perspective,* p. 43, 1957); three have escaped from cultivation; and one is a form of a species listed by the Hanes. Others are elements in old-field succession or ground-cover in wooded areas.

The list of additional species, with collection locations, habitat notes, and abundance data, follows. The nomenclature is that of Fernald (*Gray's Manual of Botany,* 8th ed., 1632 pp., 1950).

PINACEAE

Juniperus horizontalis Moench. Creeping Juniper.—Infrequent. Old-field succession. North-east quarter of the south-east quarter, section 21, Ross Township. (T1S:R9W).

LILIACEAE

Polygonatum canaliculatum (Muhl.) Pursh. Channelled Solomon's Seal.—Infrequent member of herbaceous ground cover in Maple-Basswood woodlot. Kellogg Forest. (T1S:R9W; Sec. 22. Ross Township).

JUGLANDACEAE

Carya tomentosa Nutt. Mockernut Hickory.—Frequent canopy tree of Oak-Hickory woodlot, north-west quarter of south-east quarter, section 6, Ross Township.

RANUNCULACEAE

Thalictrum polygamum Muhl. Tall Meadow-Rue. — Frequent. Wet-meadow along Agusta Creek, Section 22, Ross Township. (T1S:R9W).

CRUCIFERAE

Diplotaxis tenuifolia (L.) D. C. Wall Rocket.—Frequent ruderal element on parking-lot fill, trailer area, Biological Station. (T1S:R9W; Sec. 6. Ross Township).

ROSACEAE

Rosa nitida Willd. Shining Rose.—Uncommon. Along bank of Agusta Creek north from Headquarters house, Kellogg Forest. (T1S:R9W; Sec. 22. Ross Township).

LEGUMINOSAE

Lotus corniculatus L. Birdsfoot-Trefoil.—Frequent along roadside banks and in mixed hay fields on Kellogg Farm. (T1S:R9W; Sec. 5, 6, 8. Ross Township).

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EUPHORBIACEAE

Euphorbia humistrata Engelm. Hairy Spreading Spurge.—Common ruderal in cracks and along edges of concrete walks of main campus, Biological Station. (T1S:R9W; Sec. Ross Township).

ANACARDIACEAE

Rhus aromatica Ait. Fragrant Sumac. Uncommon. High ground above west bank of Wintergreen Lake. North-east quarter of south-east quarter, section 8, Ross Township. (T1S:R9W).

Rhus glabra L. *forma laciniata* (Carr.) Robins.—Infrequent. Border of Oak-Hickory woodlot, north-west quarter of south-east quarter, section 6, Ross Township. (T1S:R9W).

CELASTRACEAE

Euonymus europaeus L. European Spindle Tree.—Infrequent. Escape in natural shrub border, top of roadcut, north of main campus, Biological Station. (T1S:R9W; Section 6. Ross Township).

LYTHRACEAE

Lythrum salicaria L. Spiked Loosestrife.—Common. South-west shore of Mud (Stony) Lake, section 22, and along low, wet, banks of Agusta Creek, south-east quarter of north-east quarter, section 21, Ross Township. (T1S:-R9W). Taylor (*The Guide to Garden Flowers*, 131 pp., 1958) considers natural stands of this species to have escaped from cultivation.

LABIATAE

Galeopsis Tetrahit L. Hemp-Nettle.—Infrequent ruderal element of flower-beds, main campus, Biological Station. (T1S:R9W; Sec. 6. Ross Township).

Hyssopus officinalis L. Hyssop.—Infrequent member of old field succession, high ground above west shore of Wintergreen Lake, north-east quarter of the south-east quarter, section 8, Ross Township. (T1S:R9W).

SCROPHULARIACEAE

Veronica chamaedrys L. Birds-eye Speedwell.—Frequent ruderal element in lawns of main campus, Biological Station. (T1S:R9W; Sec. 6, Ross Township).

CAPRIFOLIACEAE

Viburnum denatum L. Southern Arrow-wood.—Common member of natural shrub border on road-cut, north of main campus, Biological Station. An escape. (T1S:R9W; Section 6. Ross Township).

COMPOSITAE

Hieracium paniculatum L. Panicled Hawkweed.—Infrequent ruderal element in flower-beds, main campus, Biological Station. (T1S:R9W; Sec. 6. Ross Township).—JACK C. ELLIOTT, Michigan State University, East Lansing (Present address: Professor of Biology [Botany]. University of Wyoming Team, Faculty of Agriculture, University of Kabul. Kabul, Afghanistan).

A Note to Rotifer Investigators

Announcement is made of the availability of the *Second Preliminary List of the World's Rotifer Students*. This list contains the latest addresses of rotifer workers. The chore of finding addresses for correspondence, exchange of data and reprints is ended. The list is free to workers in this field. Write to: Dr. John J. Gallagher, 1716 E. Terry, Pocatello, Idaho.

A Note Refuting the Suggestion That Some Crayfishes of Northern States Spawn in Winter

There is a seemingly widespread belief that the crayfish *Cambarus b. bartoni*, and also crayfishes of some other species as well, spawn throughout the winter. This belief probably stems from the 1906 paper of Arnold E. Ortmann (*Mem. Carnegie Mus.*, **2**:343-533). Collecting in Pennsylvania, Ortmann found ovigerous *bartoni* females in July and August, and females bearing young in March, August, September and November. In February of 1898, at Princeton, N.J. (the date was not recorded, but was given as towards the end of the month), Ortmann also found a *bartoni* female carrying young. To the writer's knowledge, Ortmann's report of a northern crayfish found with young in winter, is singular, not only for *C. b. bartoni*, but for all northern crayfish.

Ortmann then suggested that the young found in February must have been in the egg stage in January, and that the lack of a December report was probably due to the incompleteness of investigations. Thus he accounted for all the winter months and suggested that *C. b. bartoni* and other "cool water" types may be expected to spawn throughout the year.

Unfortunately, Ortmann gave no details about his winter find, save the general area (Princeton, N. J.), and roughly, the time of the month. He did, however, state that there were only ten young, and he suggests that other young may have escaped. This also suggests, however, that these young were probably well advanced in their development.

On February 27, 1959, the writer found a *C. b. bartoni* female with young in Catatonk Creek, a few miles north of Candor, Tioga county, New York. This creek is a good collecting place for *C. b. bartoni*. The creek was covered with ice from bank to bank in places, but the collecting area was extensively open, with but a bit of ice along the banks. The water temperature was 5.5°C., and the water flow was moderate. The female with young was the eleventh crayfish collected that day. All were very immobile, made no active movements, and were simply picked up from the bottom by hand, after turning the stones that sheltered them.

The female and young were immediately taken to the laboratory and there placed in a tank of water at room temperature (19°C.) after allowing for a gradual warming. In the warm tank water, the female was immediately quite active, and thereby dislodged all of the young, numbering 41. The young were scattered about the two-gallon tank, and 16 hours later were still scattered, none being attached to the female which remained under a rock shelter.

Four young were removed and preserved. They were heavily pigmented, very hairy, and very "dirty" in appearance as is indicative of crayfishes that have not recently molted. They ranged in size from 5.2 to 5.5 mm carapace length, had a five-membered tail fan, and in three young, the first pleopods were just in evidence as buds. In addition, all four young had numerous growths on their exoskeletons of a colonial ciliate, probably *Epistylis cambari*. These growths may also be indicative of crayfish immobility and of a recent lack of molting.

Considering the inactive state of all of the 11 crayfish collected at this time, and the size, stage of development, and general appearance of the young, it is difficult to believe that these young were spawned sometime during the winter, and then underwent a number of molts. It would seem that the possibility must be considered that these young were oviposited in the fall, and had

hatched but were still with the female parent when cold water temperatures immobilized the female and her attached young, and thereby arrested the development of the young. Ortmann did not consider this possibility in his paper, but it is here suggested that the young he found in February were also spawned in the fall, and not in January as Ortmann suggested. If any northern crayfish do oviposit, hatch and rear young through the winter, it remains to be substantiated.—LAWRENCE R. MCMANUS, Cornell University, Ithaca, New York.

The Pronghorn, Antilocapra americana, in Western Iowa

Nelson (Bull. U. S. Dept. Agric., 1346:2, fig. 1, 1925) and Hall and Kelson (The mammals of North America, p. 1023, fig. 495, 1959) mapped the former distribution of the pronghorn, *Antilocapra americana*, as extending eastward to extreme western Iowa. The occurrence of the species in that state has, however, never been documented in the scientific literature; nevertheless, there is an historical record of the pronghorn in western Iowa.

In the spring of 1850 T. A. Culbertson left St. Joseph, Missouri, by horseback with a small group of companions and traveled along the Iowa side of the Missouri River, headed for the badlands of South Dakota and the Upper Missouri region (see Culbertson's account, "Journal of an expedition to the Mauvaises Terres and the Upper Missouri in 1850" edited by J. F. McDermott, Bull. Bureau Amer. Ethnol., 147:viii + 1-164, 1952). The party traveled mostly on the "rolling prairie" just east of the Missouri River. On April 7, 1850, in what is now western Harrison County, Iowa, Culbertson wrote (p. 30): "To-day we passed Willow Creek, two forks of the Soldier River, and the main branch itself, and are now on the bank of the Little Sioux [River] ready to cross it in the morning. Had some elk meat for dinner to-day *and the men saw four antelopes* [italics mine]." On the following day the party crossed the Little Sioux, which took until noon, and during the course of the afternoon in northwestern Harrison County or southwestern Monona County saw (p. 31) ". . . *several antelopes in full flight . . . along the prairie* [italics mine]." The areas in Harrison and Monona counties where pronghorns were seen are between 41° 30′ and 42° 00′ north latitude, and are opposite Burt and Washington counties, Nebraska.

Probably the Missouri River, or more precisely its deciduous riparian association, served as a barrier to the distribution of pronghorns at the latitude of Iowa and Nebraska. Farther to the north in southern and central South Dakota, however, the deciduous association along the river became narrower, and even discontinuous in some places. Here no barrier to the dispersal of pronghorns existed and the species ranged eastward to southwestern Minnesota (Hall and Kelson, *op. cit.*:1022) and southward on the eastern side of the Missouri into western Iowa. Other reports of occurrence of pronghorns in western Iowa probably are in the historical literature dealing with that area. —J. KNOX JONES, JR., Museum of Natural History, University of Kansas, Lawrence.

Book Reviews

GEOLOGY OF THE GREAT LAKES. By Jack L. Hough. The University of Illinois Press, Urbana, Illinois. 313 pp., 75 figs. including 26 lake stage maps, 22 tables. 1958. $8.50.

This book gives a comprehensive account of the origin and history of the five Great Lakes of North America. Dr. Hough was selected as the recipient of the Kirk Bryan Memorial Award presented by the Geological Society of America for this work "which represents a modern interpretation of the late Pleistocene and post-glacial history of the lakes." Geologically speaking, lakes such as the Great Lakes are ephemeral. They came into existence some 15,000 to 20,000 or more years ago with the wane and retreat of the last continental ice sheet. Resting on a truncated bedrock surface which ranges from Precambrian to Carboniferous rocks, the Great Lakes developed between land and ice with increments of differential erosion and deposition through the energy of water — streams, waves, currents, and other periodic fluctuations. It is this recent geological history gathered from a fragmentary record which is complex and difficult to decipher in the detail that is indicated in the book.

In 1915 the United States Geological Survey published Monograph 53, Leverett and Taylor's classic "The Pleistocene of Indiana and Michigan and the History of the Great Lakes." During the intervening 43 years, much research has been and is being done on the geology of the Great Lakes so that Hough's full treatment is most welcome. Hough started research on this subject in 1932. The bibliography lists 7 publications on Great Lakes geology which he has contributed.

The book is written in two parts. The first part discusses the Great Lakes region, present lakes and pre-lake history, and methods of dating events of lake history. Much factual physical data is given concerning areal size of lakes, depths of water, bottom topography, geological setting, dynamics and chemistry of lake water, a brief discussion of lake sediments and a condensed account of pre-glacial and glacial history of the lakes with an introduction to methods of dating such chronology. Laymen and scientists working in related fields will find much information and handy reference in this portion of the book.

The second part deals with a well-documented interpretation of the detailed chronology of lakes development. The history of the individual lakes is correlated and integrated into the history of the entire Lakes. This part of the book discusses drainage directions, outlets, and changes, high and low water stages, beach development and hinge-line changes due to isostasy.

The author has summarized in chart form (table 22) the correlation of events of Great Lakes history with absolute chronology based upon radiocarbon dates. He has made this more graphic and understandable by including 26 lake stage development maps which take them from the time the basins were occupied by continental glacial ice through their high and low stages to the present modern Great Lakes. The book concludes with an excellent bibliography of 231 references which gives the reader basic sources for much of the information used.

Hough's interpretations based upon sound principle are forthright and admittedly tentative. Printing costs undoubtedly limited the book's content but several omissions are noted. It needs the perspective of a large scale map covering the entire area of the lakes. Information given for single lakes such as the bottom topographic configuration and current directions could have been compiled on the larger map along with the bedrock geology including specula-

tive projection of the formations under the lakes, hinge lines, dunes areas, etc. Other things not included cover information and references to dunes areas some of which are classic, discussion related to the engineering aspects of the lakes, more on the biology and sediments of the lakes, rates of ice retreat, and inclusion of authors in the index for reference checks.

The book is directed primarily to the geologist but since the lakes are used for water supply, navigation and transportation, food supply, recreation, and are involved in various conservation and engineering projects, other people will find the information useful. Biologists, particularly limnologists, ecologists, and conservationists, along with engineers, will find much basic data and history closely related to their interests.

The symposium on the Great Lakes conducted by the Geology and Geography section of the American Association for the Advancement of Science at the annual meeting in Chicago, December 28-29, 1959, is a recent sequel to Hough's book.—RAYMOND C. GUTSCHICK, Department of Geology, University of Notre Dame, Notre Dame, Indiana.

POISONOUS AMPHIBIANS AND REPTILES RECOGNITION AND BITE TREATMENT. By Floyd Boys and Hobart M. Smith. C. C. Thomas, Springfield, Illinois. 149 pp. 1959. $4.75.

The authors treat a very difficult and admittedly confusing problem in an interesting though sometimes prolix manner. The subject matter is divided into nine parts. Included are sections on the taxonomy of venomous animals, the chemistry and mode of action of the poisons of certain amphibians and reptiles, and the first aid and medical treatment for the injuries inflicted by these animals. The sections on the general zoological characteristics of venomous reptiles, general precautions against snakebite, and the recognition and distribution of venomous animals are accurate and adequate. The drawings, pictures and maps are well done. The various sections dealing with the chemistry, mode of action of the poison and treatment of the envenomated victim are somewhat of a *mare liberum* and will raise a number of Hippocratic eyebrows.

Snake venoms are complex mixtures, chiefly proteins, many of which have enzymatic activity. The lethal effects of snake venoms are probably due to the non-enzymatic proteins, though the enzymes and enzymatic combinations certainly contribute to the over-all toxicity of the poisons. In addition to the separate and combined activities of these substances, and the metabolites formed by their inter-reaction, the envenomated organism is capable of releasing several autopharmacologic substances which may complicate the mode of action of the venom, and may render treatment of the victim more difficult. The more important fractions of rattlesnake venom are crotoxin, crotactin and crotamine, rather than the enzymes noted in the book. Unfortunately, the authors have overlooked these generally accepted working hypotheses as well as the many splendid contributions on the physiopharmacology and chemistry of snake venoms by Habermann, Neumann, Frankel-Conrat, Goncalves, Moussatche, Slotta, Kaiser, Michl, Fischer, Raudonat and others. The "physiological fractions" outlined by the authors will no doubt shake-up many zootoxicologists working with the snake venoms. It is a common error for all of us to divide our limited knowledge into even more limited segments for the purpose of classification, or under the pretense of bidding for clarity. The arbitrary division of snake venoms into such classifications as neurotoxins, hemopathogens, cardiotoxins, hemotoxins, hemorrhagins, coagulants, anti-bactericidins, cytolysins, and some 40 other classifications given by various writers, is unfortunate. While these classifications may serve some useful purpose it is becoming increasingly

apparent from zootoxicological and chemical studies that neurotoxins can, and often do, have cardiotoxic and/or hemotoxic activity; cardiotoxins may have neurotoxic and/or hemotoxic activity; and hemotoxins may have the other activities, etc. Until the fractions responsible for the deleterious effects have been isolated and studied individually and in combination, one must consider all reptile venoms as substances capable of producing several important changes, sometimes concomitantly in one or more of the organ systems. The authors' survey of the chemical and zootoxicologic properties of venoms lacks a critical analysis of these problems and leaves much to be desired.

It will be a little disappointing to those who purchase the book with the thought of obtaining a balanced summary of the therapeutics of poisonous amphibians and reptiles to find that in the section on, "Medical Treatment in Cases of Snakebite," no data is given concerning the authors' personal experience with these injuries. As a result, many of the questions usually asked by physicians faced with the care of an envenomated victim have been overlooked. The data contained in the chapter deal with advice given by several competent physicians but the choice of material is, in the reviewer's opinion, sketchy and very partial. The condemnation of cryotherapy is unfortunate. The critical reader will find the references to unevaluated personal correspondence, used in support of various data, somewhat disconcerting.

It is true that there is no single volume dealing specifically with the material presented in this monograph. The excellent books by Klauber, Pope, and Kaiser and Michl provide most of the compiled information relative to this problem. The present volume should have its biggest appeal to campers, sportsmen and first aiders.—FINDLAY E. RUSSELL, Los Angeles County Hospital.

OBLIGATORY AND FACULTATIVE INSECTS IN ROSE HIPS. By W. V. Balduf. Illinois Biological Monographs, vol. 26. vi + 194 pages, 53 figures. University of Illinois Press, Urbana, Ill. 1959. Price, paperbound $3.50, clothbound $4.50.

This volume contains the results of a research project which extended over almost 30 years, but began with some casual observations. Dr. Balduf first became interested in the phenology of the rose curculio, *Rhynchites bicolor*, which he observed on the developing hips of cultivated roses growing on the University of Illinois campus. Later he observed some honey-yellow chalcids ovipositing in the rose hips in June. Seeking to discover something about the range of this chalcid, he picked some rose hips in northern Minnesota in September. When he returned to the university and opened the package of rose hips in October, he found that the hips had yielded neither weevils nor chalcids, but dipterous puparia. The following year in Minnesota he found a lepidopterous larva sharing the fleshy coat of rose hips with the dipteron.

He had, thus, found that rose hips in Illinois and Minnesota are inhabited by 4 species of phytophagous insects — later he found a second chalcid, which raised the total to 5. But these 5 phytophagous species proved to make up only a small part of the complex of species associated with the rose hip microcommunity. He embarked on an intensive investigation of the insects of rose hips, and this study produced 45 different species. Of these, 30 are directly associated with rose hips, while the other 15 are incidental.

The 30 species dependent on the rose hips are arranged thus: Phytophagous species which feed on the living substance of the hips, predatory and parasitic species which attack some stage or stages of the phytophagous ones, and scavengers which feed on the wastes left by those in the first two categories.

In all Dr. Balduf studied hips from 32 species or varieties of roses. Most of his rose material came from Minnesota, Wisconsin, and Illinois, but he also

secured rose hips from the area from Alaska, the Prairie Provinces, Ontario, and Maine in the north, south to California, Mississippi, and North Carolina. He reared over 14,000 adult specimens, and additional thousands of larvae, taken from the hips, were dissected to secure the immature stages of their endoparasites.

The bulk of the pages in this volume are devoted to careful, detailed studies of the habits and life histories of the individual members of the rose-hip complex. Dr. Balduf secured for study and description the eggs, larvae, and adults of almost all the species encountered in this investigation. Along with the accounts of these, a thorough coverage of the existing literature, if any, about them is given. Needless to say, almost all the information given in this study is new. Many of the insect parasites which he found had to be described before names for them were available for use in this book.

This volume includes a bibliography and excellent drawings of the adults and immature stages of most of the insects discussed in the text. The drawings are the work of Donald Van Horn.—B. D. Burks, Entomology Research Division, U. S. Department of Agriculture.

PLANT PROPAGATION: PRINCIPLES AND PRACTICES. By H. T. Hartmann and D. E. Kester. Prentice-Hall, Inc. 559 pp. 1959. $8.75.

This interesting and useful book provides, in the authors' words "a source of information concerning the fundamental principles involved in plant propagation and serves as a manual that describes useful techniques for propagating plants." The physiology and anatomy of seed selection, seed propagation, cutting, grafting, and budding are treated in separate chapters. Each chapter of more or less theoretical material is followed by one or more chapters of detailed descriptions of technique. The illustrations are numerous and well conceived, if rather small in execution. There are many references. The final section of the book considers briefly, too briefly, the particular techniques of propagation that are applicable to fruit and nut trees, to ornamentals, to annuals, and to herbaceous perennials.

The book apparently is intended primarily for a course in horticulture, and its material reflects the content of such a course. Botanically, the coverage of the book is far more limited than its sweeping title would indicate. Large groups of vascular plants are neglected, *e.g.*, the ferns and fern allies, the succulents, and the aquatics. There is no discussion of the propagation of thallophytes and bryophytes. The usefulness of the index suffers from an almost total exclusion of scientific names. It is easy to dwell on what is omitted and to praise what is included.—G. T. A. BENDA, University of Notre Dame, Notre Dame, Indiana.

A THOREAU HANDBOOK. By Walter Harding. New York University Press, 213 pp. 1959. $4.50.

This *Handbook* will prove invaluable to anyone who reads Thoreau with pleasure, as the plan of the book makes evident immediately. The book contains, first, a Thoreau chronology for ready reference, then five chapters entitled respectively, "Thoreau's life," "Thoreau's works," "Thoreau's sources," "Thoreau's ideas," and finally "Thoreau's fame," a study of the changing attitude toward Thoreau from his lifetime to the present. Each of these chapters is divided into two sections, the first of which provides a heavily, but unobtrusively, documented running account of the topic treated, and the second of which is a critical bibliography on that topic. These bibliographies include accounts of doctoral dissertations and some masters' theses which are not in print, and

in many cases provide brief summaries of the chief contributions of such works. In short, the book is a compendium of years of intensive Thoreau scholarship made available to anyone interested in Thoreau. More succinctly than any other source it defines Thoreau's present position in literary, scientific and political thought.

Naturalists are likely to be most interested in the chapter on Thoreau's ideas and discussion of his contribution to the science of his day and ours. Harding cites several uses of Thoreau's records by recent scientists, and adds that he understands that Thoreau's weather records in the *Journal* are even now being scrutinized by the American Meteorological Society. Harding feels that Thoreau, however much he protested against the confines of science as he knew it, became increasingly scientific in his concern with such data as species lists and water temperature records, and that his material has proved of value to modern scientists.

The bibliography included with this chapter is the fullest record of the evaluation of Thoreau's science yet printed; although the amount of space devoted to Thoreau as a scientist is small, as it should be, since Harding is interested in illustrating Thoreau as the multifaceted man that he was.

Probably Harding's major achievement in the *Handbook* is the objectivity and sense of proportion which the book reflects. The whole *Handbook* makes a determined effort to see Thoreau whole and avoid partisanship with any school of Thoreau interpretation. At the same time he sounds the necessary warnings that Channing's *Thoreau the Poet-Naturalist,* while it provides a great deal of source material, fails to properly identify quotations and is not always accurate in its facts; that Sanborn, who like Channing had the advantage of personal acquaintance with Thoreau and Concord, perhaps for that reason, felt free to alter Thoreau's writing to bring it into accord with his own standard of decorum; and that although Canby's biography added many new facts to our knowledge of Thoreau, his assertion that Thoreau was unconsciously in love with Lidian Emerson rests upon unscholarly evidence.

In view of the widespread disagreement as to whether or not Thoreau's life proved ultimately satisfying to him, it is important to note that Dr. Harding who is conspicuously without "a chip on his shoulder" or "a thesis in his hand," whose Thoreau work has been both extensive and remarkably free of the curse of thesis, records that "Canby looked upon Thoreau as the happiest man of the Concord group. It is my opinion that Canby is closest to the truth on this point," and on page 167 he writes "Basically Thoreau's life was a happy one."

The chapter on "Thoreau's Fame" will be of interest to naturalists chiefly because it demonstrates how recently interest in Thoreau as a scientist has developed. — KATHRYN AND PHILIP WHITFORD, University of Wisconsin, Milwaukee.

A REVIEW OF THE SIRENIA AND DESMOSTYLIA. By Roy H. Reinhart. University of California Publications in Geological Sciences, Volume 36, No. 1, 146 pp., 19 figs., and 14 plates. 1959. $3.00.

Reinhart has apparently devoted a great deal of time and energy to this fairly extensive revision of the orders Sirenia and Desmostylia. All Sirenian fossils reported from the east and west coasts of North America, from the Caribbean and the west coast of Mexico are reviewed, and the more important European and Egyptian specimens are compared with the Western Hemisphere forms. It is shown that the family Dugongidae has had a world-wide distribution in the past and that the family has experienced a moderate diversity of form as compared to that found in the family Trichechidae. Reinhart's suggestion that the family Dugongidae was early split into two phyletic lines start-

ing with the middle Eocene *Eotheroides* is quite reasonable.

It is indeed gratifying to see a paleontological publication in which the truly indeterminate nature of much of the sirenian material from eastern United States is regarded as such. The stratigraphic and correlational problems associated with the Ashley River beds of South Carolina and the Calvert formation of Maryland are adequately emphasized. However, it is unfortunate that the author, in discussing the Dugongidae of Florida, does not mention a similar problem in regard to sirenian remains from the Bone Valley Gravel formation of west central Florida. At least some faunal elements of the entire assemblage of vertebrates obtained from this formation are definitely Miocene, while others seem to be Pliocene. In addition, superficial beds have yielded well-known Pleistocene forms. Most of the marine vertebrates from the formation appear to be Miocene in age while most of the terrestrial forms are presumably Pliocene. Thus, the Bone Valley Gravel felsinotheres may be Miocene rather than Pliocene. It is also unfortunate that, although the type locality of almost all of the more important fossil specimens is given, there is no locality or formation mentioned in reference to either *Felsinotherium ossivalense* or *F. floridanum*.

It may have been a little easier for the reader had the author not interspersed his discussion of the known sirenian fossils of various areas in the New World with descriptions of new genera and new species. It is also unfortunate that in a monograph of this scope the Order Desmostylia is not as thoroughly reviewed as the Order Sirenia. *Cornwallius* might have been profitably discussed in somewhat more detail. Reinhart gives a very fine synopsis of the familial and sub-familial characteristics of the various groups included within the Order Sirenia. It would have been to some advantage to have had a similar synopsis of the familial characters of the Desmostylia at the end of that section. He might also have included a more thorough discussion of the evidence bearing on the advisability of erecting a new order of mammals. No true diagnosis of the order exists in the review, and the reader must refer to a previous single-paged paper published six years ago in the *Journal of Geology*.

The drawings throughout are well-chosen with respect to position and are well executed. On the whole the plates are very good. although some of the elements, particularly several of the more important limb bones of *Desmostylus* and/or *Vanderhoofius* might have been shown to better advantage in line drawings.

New taxons described include *Caribosiren turneri*, n. gen. et sp., *Halianassa vanderhoofi*, n. sp., *Vanderhoofius coalingensis*, n. gen. et sp., and *Paleoparadoxia tabatai*, n. gen. All previously described species of *Desmostylus* are placed in the synonymy of *D. hesperus*.

The publication is quite thorough, and provides considerable evidence that Reinhart is well qualified to judge the systematic value of the distinctive characters of the described forms. Although the specialist may find a few points with which he disagrees, the monograph is most certainly a valuable contribution to our knowledge of these Tertiary marine forms. — WALTER AUFFENBERG, University of Colorado, Boulder.

THE PHENOMENON OF MAN. Pierre Teilhard de Chardin. Harper & Brothers. 318 pp. 1959. $5.00.

There is something stimulating in perusing a book that has been suppressed; perhaps that is one of the reasons *The Phenomenon of Man* seems more noteworthy than similar volumes dealing with the evolution of life that recently have been published. Frankly teleological and concomitantly monistic, the manuscript was composed by the Jesuit paleontologist, Pierre Teilhard de

Chardin, during the years 1938-1940. However, his religious superiors thrice forbade publication of this document, although he did publish other works until his death, notably *Le Groupe Zoologique Humain* and *La Vision du Passe.* Fortunately, Père Teilhard left his manuscripts to a friend so that the book could be released after his death in 1955 when permission to publish was no longer required. Originally published as *Le Phenomene Humain* in France where it was the best-selling nonfiction book of the year 1955, the English version has been expertly translated by Bernard Wall.

In an attempt to produce a synthesis of the emergence of life which will culminate in the sharing of all life in the Omega, which is the end point of evolution according to Père Teilhard, both the biological and psychical development of nature is considered. All matter is held to possess a certain degree of consciousness. This consciousness emerges more distinctly in the instincts of man and achieves its climax in the human organism with the appearance of reflective thinking. Man, however, is not merely a more highly individualized organism. Man is a person — one who has transcended individuality in personality.

This individualization and personalization depends on the cephalization of the unfolding organism, since it is the head that contains the main organ of coordination or brain. As Sir Julian Huxley points out in the introduction, Père Teilhard stresses that the process of evolution on earth is itself now in the process of being cephalized. Evolution is at last becoming conscious of itself in that man is the first product of evolution to appreciate the very process which has developed him. But in man evolution is characterized more by cultural than genetic or biological change. Therefore, our concept of evolution has to include what is termed a "psychosocial process." This is a complex of factors which have produced cultural differentiation. Various groups resulting from this process are not considered as sharply delineated as biological species. Man is the only successful type of life to remain a single interbreeding group. Today there is a tendency towards cultural convergence resulting in a movement of the whole human species into a single interbreeding group based on a unitive, self-developing framework of thought — the noosystem. (Gr. *noos* — thought.) From this the author expands his concept to that of a noosphere or thinking membrane with which man has overlaid the biosphere or life layer of the earth. The noosphere incorporates the cosmos, including its trend in direction and time, as well as the psychosocial processes existing on earth. This makes of the noosphere a microcosm, including both the knowledge of the universe as well as the unification, with increasing intensity, of the system of human thought. And this will result in the Omega point, where the noosphere will achieve its essential unity and become a hyperpersonal organization.

Indeed, this volume requires more than ordinary concentration to grasp, particularly since the author is prone to sentences which are occasionally almost a page in length. At other times, what appear at first glance to be merely disjointed phrases are interspersed among the elongate sentences. Yet, *The Phenomenon of Man* is a remarkable integration of evolutionary data with religious principles and certainly is worth the effort needed to thoroughly digest its contents. Since there are reputed to be three more books of Père Teilhard's yet to be published, we can hope that these will clarify some of the unique concepts that are embodied in *The Phenomenon of Man.*

The epilogue entitled "The Christian Phenomenon" should more properly be reviewed by a competent theological authority, since some of its conclusions are as unusual as the opinions expressed in the preceding chapters.—BROTHER G. NICHOLAS, F.S.C., Department of Biology, University of Notre Dame, Notre Dame, Indiana.

INSTRUCTIONS FOR AUTHORS

Manuscripts should be typewritten, double-spaced, with ample margins, on one side of 8½ x 11 inch paper. Tables and figures should be placed at the end of the manuscript. Each sheet should be numbered consecutively. The title and author's name along with the full mailing address of the author should be placed on the first page.

Style, arrangement, spelling, and abbreviations should conform to the usage of recent numbers of this journal. Do not underline any words except scientific names. Acknowledgments can be included in the Introduction, or may be offered as a footnote attached to the title of the article. Papers should be concisely written. A subsidy will be required for papers which exceed twenty journal pages in length.

References should be listed alphabetically by authors' names. In the text they should be cited by author and date, e.g., Smith (1958). The form of the citations should be that used in this journal; in references to papers in periodicals, titles should be given and inclusive page numbers are required. All citations should be checked with the original articles. Abbreviations of the names of periodicals should conform with the listings in BIOLOGICAL ABSTRACTS 29(5):v-xxxv (May, 1955), or 30(5):xi-xxxii (May, 1956). Book citations should include author's name, complete title, edition, name and location of publisher, and total number of pages.

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